THE EFFECTS OF DIFFERENT BURNING REGIMES ON GRASSLAND PHYTODIVERSITY

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Cover: Looking out across the *Themeda triandra* dominated grasslands of the Mlambonja Wilderness Area, towards Cathkin Peak (Mdedelelo) from the Cathedral Peak research area in the KwaZulu-Natal Drakensberg, South Africa.

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ABSTRACT

The southern African grassland biome has a diverse flora including many rare and endangered species deserving a high conservation priority. With less than two percent currently conserved, proper management of this biome is crucial to maintaining its diversity. Fire, in particular, is important and although there has been extensive research into the grazeable component of the sward, little attention has been paid to the effects of burning on forbs or the overall phytodiversity.

The aim of this study was examine the effects of different burning regimes on grassland phytodiversity. To do this, three long-term burning trials, widely located across the biome and consisting of a range of treatments randomly allocated to plots in replicated block designs, were sampled. Manipulated according to the frequency and season of burn, with fire protection controls, diversity was sampled at different scales across a range of treatments. In addition, a range of sward attributes was sampled in an attempt to explain diversity patterns.

Diversity was sampled at each site using the importance-score method. This provided measures of the species richness and rare species (species occurring in ≤ 3 plots). The effect of frequency and season of burn on species richness was then used to test the predictions of the intermediate disturbance hypothesis (IDH). Ordination techniques and dissimilarity comparisons were used to compare the species composition between the replicates of each treatment and between treatments. Effects of the different treatments on vegetation patchiness were also examined at the plot scale at each site and beta diversity sampled at one of the sites. Species richness was also related to the biomass sampled at each site and calculated from the relationship between rainfall and biomass across the biome. Further, the response of a range of sward attributes, including: percentage cover, light attenuation and biomass, to the burning treatments was examined. Due to the lack of basic biological information on the grassland forbs, the taxa recorded at each site were tabulated by family, and the underground organs of the forbs examined.

Results from the three study sites indicated that measures of species richness were scale dependent and differed between sites, but provided no conclusive support for the IDH. Nevertheless, there was evidence for a hump-backed relationship between species richness and biomass sampled at each of the study sites. In the absence of post-burn successional differences, results indicated that species composition of the grasslands was responding more to environmental gradients than to the long-term application of the burn treatments. However, aerial cover was dominated by a few grass species that showed clear responses to the frequency and season of burn. These results may be explained by the large proportion of forbs that possessed underground storage organs which buffer forbs against variations in fire frequency and season. It is predicted that these storage organs, that are common to plants in fire prone systems, allow forbs to cope with different burn intervals and seasons.

Results also showed that directional changes with fire protection were favouring a different suite of species to those found under burning, and may therefore be used to increase landscape diversity. Vegetation patchiness showed no clear trends according to the burning treatments in the plot studies, but beta-diversity results suggested that heterogeneity may increase with burning intervals. Light attenuation down the sward was found to differ with the time since last disturbance rather than the frequency of burn. Sward biomass, however, appeared to increase with longer burn intervals, but did not clearly respond to the season of burn.

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EASTERN CAPE:

KWAZULU-NATAL DRAKENSBERG:

GENERAL:

LIST OF ABBREVIATIONS

1y - annual burn, burnt every year
2y - biennial burn, burnt every second year
3y - triennial burn, burnt every third year
4y - quadrennial burn, burnt every fourth year
5y - quinquennial burn, burnt every fifth year
6y - sexennial burn, burnt every sixth year
8y - octennial burn, burnt every eighth year
FP - fire protection, treatments not burnt at all
Sum - summer burn
Aut - autumn burn
Win - winter burn
Spr - spring burn
Spr H - spring hot (high intensity) burn
AD - *Anno Domini*, 'in the year of the Lord'
BP - before the present
ca. - *circa*, about
C - catchment
CA - correspondence analysis
CCA - canonical correspondence analysis
F - average cumulative total leaf area per unit ground area
FB - fire-break
IDH - intermediate disturbance hypothesis
PAR - photosynthetically active radiation
TP - transect pair, paired transects in the catchment and fire-break
$\bar{x}$ - sample mean
S_x - standard deviation

Figure 1.1.

Centre:

Distribution of the southern African grassland biome, with labels indicating the location of the three study sites within the biome.

Pictures clockwise from top left:

1. Montane grasslands of the KwaZulu-Natal Drakensberg, taken from the top of catchment X (±2000m) (biennial spring burn) at Cathedral Peak.
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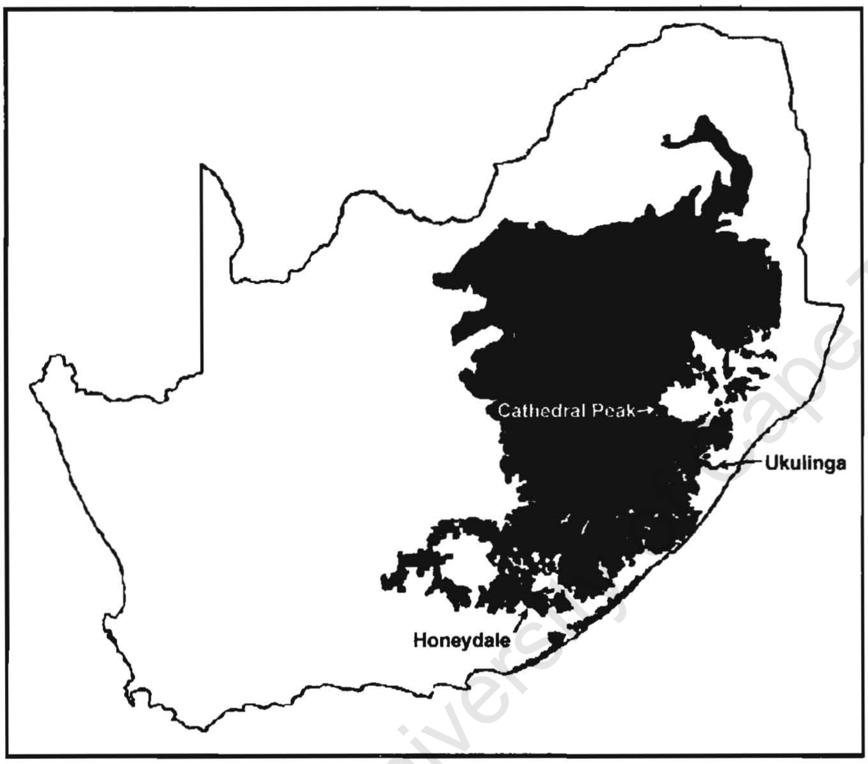
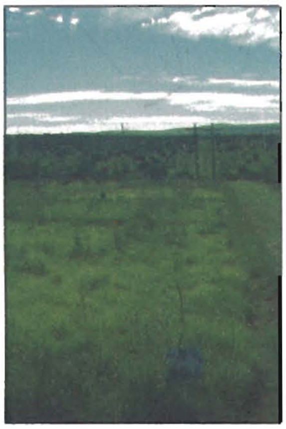
BROTH ERTON


Cathedral Peak
Ukulinga
Honeydale



INTRODUCTION

1.1 BACKGROUND TO THE STUDY

The southern African grassland biome has an extremely rich and diverse flora including many rare, endemic and endangered taxa (Gibbs Russell 1987; Cowling, Gibbs Russell, Hoffman & Hilton-Taylor 1991; Scott-Shaw 1999). The biological diversity of these grasslands is, however, seriously threatened by an ever increasing human population and its accompanying industrialization, urbanization and agricultural demands (Rutherford & Westfall 1994; O'Connor & Bredenkamp 1997). Currently, less than 2% of this biome is being conserved (Rutherford & Westfall 1994) and there is limited scope for improving this percentage in the immediate future. This is largely due to a lack of funding and suitable, available land to create new conservation areas. Thus, the 2% of grassland biome that is currently conserved needs to be adequately managed to maintain its diversity. Fire plays an integral part in this management, but most of the research on the ecological consequences of fire in these grasslands has had an agricultural focus, phytodiversity being largely ignored. It has therefore become important to investigate the effect of different burning regimes on the entire floristic wealth of this region.

1.2 WHAT IS BIOLOGICAL DIVERSITY?

Although well known and used, the term, biological diversity (biodiversity), is often ill-defined. Biodiversity is generally understood as the total variety of living organisms that exist on this planet (Stuart & Adams 1990). What is usually overlooked though, is that variety (diversity) is largely an intuitive measure, composed of several components (West 1995). It is the combination of these components that influences our understanding of what may be termed diverse.

The simplest way to describe diversity is to count the number of different genes, species or habitats whose diversity is being measured (Rosenzweig 1995). However, a community with five equally abundant species cannot be considered to have the same diversity as a community with the same five species, one of which comprises 95% of the individuals (Peet 1974); this is the concept of evenness. Species evenness in a community is a measure of the relative distribution of individuals among the different species in that community. The more equal the numbers of individuals of each species in the community, the greater is the diversity as perceived intuitively (Huston 1994). Thus, species diversity is fundamentally a function of the number of species and their evenness in the community (Schluter & Ricklefs 1993).

As species differ in their perceived value, so to does their relative importance in describing the diversity of an area. Extinction, as a natural occurrence, results from accidents or population interactions. Given time, all species will eventually succumb to an accident and go extinct (Rosenzweig 1995). Yet, human interference has greatly accelerated extinction rates, making it necessary to provided higher conservation status to species that are in danger of becoming extinct (Huston 1994). Species that have small population sizes and/or restricted geographical areas or habitats are considered to be most at risk (Rosenzweig 1995). Such species are thus important in describing the diversity of an area because of the need to conserve them. Diversity therefore assumes a further component to indicate that although rare and endemic species may not have high diversity values, according to numbers and evenness, they require special conservation status.

One of the difficulties in defining diversity is that it varies according to the spatial and temporal components of the measurement. The size of the area to be sampled will directly influence the measure of diversity; a fundamental rule of biology being that as the sample area or intensity increases, so too will the number of species. In addition, the spatial scale of the sample also influences variability in physical and biological factors which may influence species diversity (Huston 1994). Changes across the temporal scale vary from fluctuating seasonal patterns in diversity to fluctuations in evolutionary time over hundreds of millions of years (Rosenzweig 1995). In groups of organisms that show seasonal diversity patterning, diversity measured at one time of the year will differ markedly from diversity measured at another time of the year. When considering succession in ecological time, species composition and diversity of a community may change gradually over time spans of several hours to several centuries, depending on the lifespans of the dominant organisms (Huston 1994). Therefore, selecting the correct spatial and temporal scale at which to assess diversity is crucial to the understanding of the patterns and processes that influence diversity.

The spatial scale at which organisms in a community are sampled is important, not only for an appropriate sample of the diversity of the organisms themselves, but for an appropriate sample of the physical and biological factors that influence species diversity. The relationship between sampling scale and the processes that influence species diversity is the basis of the distinction between 'within-habitat' and 'between-habitat' diversity (Huston 1994). Whittaker (1972) recognised that the total diversity within a region (gamma diversity) could be partitioned into two components: local (alpha) diversity and the turnover of species between habitats or localities (beta diversity) (Schluter & Ricklefs 1993). Alpha diversity was first described as 'point' diversity. MacArthur (1964) introduced the concept of point diversity to determine how much of the diversity of the birds he was sampling was due to vertical zonation. Thus he was able to separate vertical from horizontal habitat complexity. Point diversity works well in that respect but, as Rosenzweig (1995) observes, what is the tree diversity of a point on which an oak tree grows? Obviously, the point diversity in this instance will be one species. So, for alpha diversity to be more meaningful, ecologists measure it as the number of species within an area of given size (Huston 1994). Beta diversity is the rate at which species accumulate in a census as the census taker moves in a straight line away from a point (Rosenzweig 1995). As the concept of point diversity has been replaced by within-habitat diversity, beta diversity becomes the turnover of species between habitats (Schluter & Ricklefs 1993). Beta diversity depends on the number of species in the habitat as well as a comparison of the identity of those species and where they occur. Beta diversity is thus expressed in terms of a similarity index between communities or as a species turnover rate between different habitats in the same geographical area (Huston 1994).

1.3 DISTRIBUTION OF GRASSLANDS

Grass-dominated vegetation types may be divided into three broad categories, the grasslands, savannas and tundra. Grasslands, as examined in my study, are characterised by a simple, single layered, herbaceous community dominated by perennial grasses (Figure 1.1). This distinguishes them from savannas where, in addition to the herbaceous community, there is an upper layer(s) of woody plants (Archibald 1995; Low & Rebelo 1996). The treeless polar and alpine tundra is characterised by a mixture of grasses, rushes and sedges, interspersed with perennial herbs and dwarf shrubs (Archibald 1995). Southern African grasslands are dominated by C_4 grass species, with C_3 species only occurring at high altitudes (Vogel, Fuls & Ellis 1978). "Sour" grasses that are palatable for only six to eight months of the year, are found in the moist grasslands (above 625mm mean annual rainfall). These grasslands tend to have leached and dystrophic soils, with high plant canopy cover, production and fire frequency. "Sweet" grasslands that are palatable year round, occur in the dry regions of the biome (below 625mm mean annual rainfall). Unlike the moist grasslands, soils in these grasslands tends to be less leached and eutrophic, with low plant cover, production and fire frequencies (Tainton 1981; Rutherford & Westfall 1994).

In Africa, the grassland biome is localized in Lesotho and South Africa. Here it occurs on the high central plateau and east of the escarpment in the inland areas of KwaZulu-Natal and the Eastern Cape (Rutherford & Westfall 1994; Low & Rebelo 1996) (Figure 1.1). These grasslands span an altitudinal gradient from sea level to >3300 m; a rainfall gradient from *ca*. 400 to >1200 mm.yr^{-1}; a temperature gradient from frost-free to snow bound in winter; and exist on a range of soil types from humic clays to poorly structured sands (O'Connor & Bredenkamp 1997).

The extent of the biome conforms to climatic factors which separate it from the adjoining Nama-karoo, forest and savanna biomes (Rutherford & Westfall 1994). Grassland, forest and savanna biomes are distinguished from the Nama-karoo biome by longer growing seasons and higher temperatures during the non-growing season. Forests require higher seasonal rainfall than grasslands and savannas, but occur in patches within the grasslands, provided there are sufficient growing days, appropriate soils and protection from fire. Savanna forms the largest portion of the grassland boundary. Climatically, savanna regions experience higher mean temperatures during the non-growth season than the grasslands (Ellery, Scholes & Mentis 1991; Ellery, Mentis & Scholes 1992; O'Connor & Bredenkamp 1997). Hypotheses attempting to explain the position of the grassland/savanna boundary include: the interacting roles of fire and anthropogenic influences (see Chapter 1.5); and the exclusion of woody plants from grasslands by seasonal water logging (Tinley 1982; Feely 1987). However, none of these explanations has been formally tested across the grassland biome. Further, the role of edaphic factors is incompletely supported by the array of soil types across the biome (Ellery & Mentis 1992).

1.4 EVOLUTION OF AFRICAN GRASSLANDS

As flowering plants, grasses probably evolved in the Cretaceous period, but the first definite evidence of their existence is found in pollen records from the Palaeocene (Muller 1981). These pollen records however, provide little indication of the rise to dominance of the grasses and the formation of grasslands (Gibbs Russel *et al.* 1990). The first evidence for the formation of grasslands appears in the dentition of herbivore fossils from the Eocene. These fossils show development of the high-crowned teeth necessary for chewing the abrasive leaves of grass plants (Stebbins 1981). Later evidence for the spread of grasslands comes from fossil grass plants which first appear in the fossil record from the early Oligocene (Gibbs Russel *et al.* 1990). The grasses with C_4 photosynthetic pathways, which now dominate the southern African grasslands (Gibbs Russel *et al.* 1990), first appeared in the middle Miocene (Jacobs, Kingston & Jacobs 1999).

In southern Africa a savanna had developed on the high central plateau by the early Pliocene, in what is now part of the grassland biome (Archibald 1995). It is predicted that the cold and wet conditions during the last glacial maximum (18,000 ± 3000 years BP) (with temperatures 8 - 10°C lower than present) would have decreased the upper limit of tree growth by as much as 1000m (van Zinderen Bakker 1978). This would have resulted in the savanna being replaced by grassland (Archibald 1995). Pleistocene pollen profiles from Wonderkrater, the Pretoria Saltpan and Equus Cave, all found in the present savanna biome, suggest that during cooler episodes grassy vegetation occupied a much greater area to the north of its present distribution (Scott 1982; Scott 1987; Partridge, Kerr, Metcalfe, Scott, Talma & Vogel 1993). Later, during a warm period in the middle Holocene (*ca.* 7000 years BP), savanna vegetation temporarily spread southwards into what is now the main Highveld grassland (Scott & Vogel 1983). On the western boundary of the grassland biome, pollen records from the present transition of the Nama-karoo to grassland indicate that grassland has alternated with semi-desert vegetation (Archibald 1995). Under cooler conditions in the late Holocene (4000 - 1000 years BP), the grassland boundary extended further west, occurring in areas now occupied by Nama-karoo (Scott, Anderson & Anderson 1997). Pollen data from several sites indicate that, apart from temporary boundary and compositional shifts (Scott & Vogel 1983), southern African grasslands have essentially been in place throughout the Holocene, and that grasslands were often more widespread during the Pleistocene (Scott *et al.* 1997).

1.5 HISTORY OF FIRE IN AFRICAN GRASSLANDS

The view that the southern African grassland biome has essentially been in place throughout the Holocene (Chapter 1.4) has not always been held. Examining the alternative hypothesis provides useful insights into the history of fire and the evolution of the flora of the grassland biome. Acocks (1953) proposed that the grasslands to the east of the escarpment in southern Africa were 'false' grasslands, of recent origin (<600 years old), being anthropogenically derived and maintained by fire. This hypothesis was founded on the reigning ecological paradigm of succession and the migration routes of Bantu-speaking iron age peoples into southern Africa put forward by Stow (1905). Based on the local climate, Acocks, and his supporters, Phillips (1973), Tainton (1981) and White (1983) predicted that the climax vegetation of the region should be forest and scrub-forest. The presence of grasslands was ascribed to a systematic destruction of woody vegetation in the region by humans over hundreds of years. Grassland was then believed to have been maintained as a fire climax vegetation, with regular anthropogenic burns preventing the succession to the true wooded climax.

HOMINIDS IN THE GRASSLANDS:

To examine the merits of this hypothesis, it is necessary to explore the relationship between humans, the environment and their influence on the fire history of the grassland biome. Hominids have been in southern Africa for at least three million years (Volman 1984; Thackeray, Deacon, Hall, Humphreys, Morris, Malherbe & Catchpole 1990; Berger 1998), with the earliest direct evidence for use of fire coming from the Swartkrans cave in South Africa, dating to about 1.0-1.5 million years BP (Brain & Sillen 1988). Yet, our knowledge of human activities, and the impact these communities may have had on the grasslands, is very limited before the Upper Pleistocene (*ca.* 128 000 years BP) (Volman 1984). However, humans are generally thought to have only become a significant fire agent in the Holocene, when plants were adjusting to contemporary climatic conditions (Hall 1984).

Evidence suggests that populations of San-like *Homo sapiens sapiens* were present in southern Africa from about 115 000 years BP (Beaumont, De Villiers & Vogel 1978). Later Stone Age artifacts only appear in the archaeological record from *ca.* 40 000 years BP (Deacon 1984). However, these early hominid populations are considered to have been too small and their technological and hunting techniques too limited to have made any significant impact on the flora before the Late Stone Age (Siegfried & Brook 1995). Stone Age peoples probably used fire as a tool to manipulate the environment by inducing flushes of edible plants and maintaining grasslands attractive to the large herds of animals which they hunted (Hall 1984). Due to seasonal changes in climate, vegetation, game movements and possibly the availability of suitable rock shelters, these nomadic peoples probably followed specific migration routes with some degree of regularity (Hall 1984). As Granger (1984) observes, this would have lead to anthropogenic fires occurring at specific times of the year in different geographical areas at fairly regular intervals.

Although there is clear evidence for early settlement in the savanna regions of southern Africa, there is no trace of Iron Age peoples in the grasslands during the first millennium AD. It is only from between AD 1300 and AD 1400 that the first signs of Iron Age settlement in the grasslands of the high central plateau begin to appear. Even then, there was a clear initial preference for grassland/savanna ecotonal sites which seemed to have supported higher populations than pure grassland areas (Maggs 1984). According to Maggs (1984) settlement on or near to the grassland/savanna ecotone would have conferred advantages in terms of livestock transhumance. In the grasslands, away from the ecotonal margins, opportunities for ecological bet-hedging in pastoralism and cultivation would not have been as great. Further, people would have been discouraged from settling in the grasslands by the limited access to wood for building and fuel. However, substitutes for these may have been provided in the form of stone for building and cattle dung for fuel (Maggs 1984).

Due to the limitations imposed on settlement in the grassland biome, it is believed that it was only by the early eighteenth century that the biome was regularly being burnt by Bantu-speaking peoples to temporarily improve grazing and aid hunting (Hall & Vogel 1980). This suggests that the period over which these peoples may have altered the vegetation of the region is substantially less than that inferred from Stow (1905). Examination of the settlement patterns and preferences of Bantu-speaking peoples in southern Africa provides strong circumstantial evidence that the grassland biome, as it is presently distributed, has been in existence for a substantially longer period than it was inhabited by Iron Age peoples (Ellery & Mentis 1992). The hypothesis that the African grasslands east of the escarpment are replaced by forest is further refuted by palynological records (Meadows & Meadows 1988; Scott 1989; Meadows & Linder 1993), and the presence of a marked centre of endemic plants in the region (Meadows & Linder 1989; Matthews, van Wyk & Bredenkamp 1993). In addition, the majority of faunal remains collected from the region, which predate Iron Age settlement in southern Africa, are of ungulates considered to be associated with grasslands (Cable, Scott & Carter 1980; Maggs & Ward 1980; Klein 1984).

DETERMINANTS OF GRASSLAND FIRE REGIMES:

To understand the effect that hominids have had on the fire history of the southern African grasslands, it is necessary to examine the factors controlling the occurrence of fire events. Fire regime is determined by three parameters, namely: weather conditions, the availability of sufficient combustible fuel and sources of ignition (Bond 1997). The prevailing climate is responsible for the atmospheric conditions necessary for the ignition and persistence of fires. Climate (rainfall and temperature), along with the topography and soil type, also determines the quantity and quality of available fuel (Granger 1984;

Everson, van Wilgen & Everson 1988). Ignition comes from one of two sources: natural (those fires not started by humans) or anthropogenic (Tainton & Mentis 1984). Of the three parameters controlling a fire regime, human influence is limited to the timing and frequency of ignitions. The ability of humans to coordinate ignition with the weather and abundance of fuel distinguishes anthropogenic from natural fire regimes. In evaluating anthropogenic effects on the fire history of the grassland biome, it is necessary to examine how humans have altered natural fire regimes in terms of the frequency and timing of ignition.

Grassland areas in southern Africa coincide with regions where the ground lightning flash density is greater than four strikes per square kilometre per year (Edwards 1984). It is not surprising then, that lightning is considered to be the most significant natural source of ignition in African grasslands (Phillips 1930; West 1965, 1971; Scott 1970; Komarek 1971). Observations by Killick (1963), Mentis, Meiklejohn and Scotchner (1974), Moll (1976) and Granger (1984) suggest that most lightning fires occur during spring and summer (September to February). But, despite many lightning strikes to ground, the rain accompanying spring and summer thunderstorms probably extinguishes most of these fires before they spread (Moll 1976; Horne 1981). Lightning started fires have been reported by Nänni (1956); Killick (1963); Mentis *et al.* (1974); Moll (1976) and Scotcher (1980). However, they caution that as these fires are very infrequent, lightning is probably not a particularly significant ecological factor in the grasslands under present conditions. Similarly, fires started by rock falls have been reported, though they seem rare and hard to confirm (Wicht 1945; Nänni 1956; Phillips 1965, 1974; Moll, McKenzie & McLachlan 1980). Though spontaneous combustion is considered a potential source of ignition, there are no records of such fires having occurred in the grassland biome.

Based on the infrequency and randomness of natural ignitions and their coincidence with areas of sufficient combustible fuel and suitable weather conditions, it may be inferred that natural fires occurred irregularly at any one site. In addition, these fires most likely burnt patches of varying intensity and size resulting in a heterogeneous fire landscape. Although early hominids probably altered the fire regime in the grassland biome, their influence would have been limited by their low numbers. Similarly, the apparent reluctance of Iron Age people in colonising the grasslands, means that significant anthropogenic influences on the fire regime in the biome are quite recent. The intensive burning practices initiated and maintained in the grassland biome since the early eighteenth century have been aimed at providing a homogeneous grazeable sward, graziers favouring regular annual or biennial burns to provide both winter and summer forage. Through these practices, humans have increased the fire frequency and altered the extent and season of burning in grasslands (van Wilgen, Everson & Trollope 1990). This has lead to questions being raised concerning the effect that such intensive burning regimes may be having on the biological diversity of a flora that developed under a more patchy and less frequent and intense fire regime.

1.6 RESPONSES OF GRASSLAND VEGETATION TO DIFFERENT BURNING REGIMES

SURVIVAL STRATEGIES:

To explore the effect of intensified burning practises on the phytodiversity of the grassland biome, it is necessary to examine how plants adapt to regular defoliation by fire. In fire-prone environments like the grassland biome, plants rely on various survival strategies. Fire-responses of each species are determined by their susceptibility to defoliation and the timing of their regeneration in relation to fire. When plants are burnt during periods of growth or reproduction, they experience a greater loss of active tissue, and because of depleted reserves, a reduced capacity for re-growth, than if burnt when dormant (Bond & van Wilgen 1996). By scheduling their activity such that the least susceptible phase in their annual cycle coincides with the main fire season, plants can escape this damage. Such seasonal dormancy, coupled with some protection of the meristems, is exhibited by numerous plants in fire-prone environments (Bond 1997).

In addition to avoidance, some plants exhibit fire tolerance in the form of resistance to, or recovery after a burn. Resistance to fire is determined by the degree to which vital tissues are protected from heat damage (Frost 1984). Many non-grass monocotyledonous plants are protected by maintaining a store of photosynthate material in underground bulbs. Grasses themselves are among the most fire-resistant components of a plant community, due primarily to their structure and patterns of growth (Booysen, Tainton & Scott 1963; Tainton & Booysen 1963, 1965a, 1965b; Tainton 1982). Because plants are often severely damaged by fire, the ability to resprout from dormant buds located in the branches, stem, root collar or in the roots themselves, is important. Dormancy in these buds is maintained by correlative inhibition which is linked to apical dominance. When this dominance is broken by removal of the apical meristem, the dormant buds regain their meristematic activity and begin to differentiate and produce new shoots (Frost 1984). There is a close correlation between the capacity to resprout and the presence of a woody subterranean stem, rootstock or lignotuber from which numerous coppice shoots develop after defoliation by fire. This well known trait is considered to be a characteristic feature of vegetation in fire-prone environments (Burtt-Davy 1922; Martin 1966; West 1971; Rourke 1972; McMaster 1976; Carlquist 1977).

REPRODUCTION STRATEGIES:

Species that are not able to survive fire by avoidance or tolerance must regenerate from seed or become extinct at a site (Frost 1984). Those species that rely on their seed germinating after fire are benefited by the combination of open space, increased availability of resources, and temporary reduction in seed predators; conditions highly favourable for seedling establishment. Seeds may be stored in a dormant state in the soil or retained on the plant, as is common to some of the fynbos plant taxa. Though fire may play a role in inducing dormant seed to germinate, little research has been done for the grassland vegetation (Bond 1997). It should be noted that obligate reseeders appear to be rare among grassland plants (Frost 1984).

In addition to inducing germination, fire is also known to stimulate flowering in some species. Post-fire flowering is common to species whose growth form prevents serious material loss in fires and who can quickly mobilize existing resources for reproduction after a fire. Such species include the geophytes, graminoids and lignotuberous shrubs (le Maitre & Brown 1992). The association between fire and flowering varies from near obligate in small herbaceous geophytes to weakly facultative in resprouting shrubs (Bond 1997). Fire, in most examples of fire-stimulated flowering, is not obligatory. The reduction in competition and increased availability of light, water and nutrients is probably sufficient stimulus alone for many species (le Maitre & Brown 1992)

When considering how fire affects the grassland flora, the species may be divided up into functional types according to various criteria. Bayer (1955) identifies two broad flowering strategies among the perennial grassland plants: namely vernal and autumnal aspect flowering. Vernal aspect plants have a short period of activity, flowering early in spring and then dying back to ground level until the next spring. Autumnal aspect plants flower later in the season, many possessing perennial above ground stems.

Most vernal aspect plants possess underground storage organs which accumulate sufficient food and water during the active period. This is necessary to carry the plant through autumn, winter and provide a reserve for resumption of activity stimulated by the increasing warmth in spring. The behaviour of the spring flowering plants is thus also related to the height and density of the spring grass cover. If the moribund winter sward is not removed and the ground is protected from the sun, the spring plants may fail to appear. Their capacity for food storage allows the vernal aspect plants to survive a few years without any leaf production. However, it is believed that if a dense grass sward is maintained for several years, the spring aspect plants would be shaded out of the sward. The first spring plants to appear are generally the shorter species. These are also the first to be shaded out by the developing grasses. As the season progresses, there appears to be a succession of ever taller species. Those that are able to trail over the grass survive until latest in the season. Thus, vernal aspect plants may be divided into groups based on their growth form, when they appear and how long they persist in the sward (West 1951; Bayer 1955).

The second flowering strategy belongs to the autumnal or aestival aspect plants which flower later in the growing season. They are taller than the vernal aspect plants and include tall herbs and shrubs. Many possess perennial above ground stems, but some, like the spring aspect plants, have perennial below ground parts only, the above ground stems dying in winter and being renewed in spring. Through their height, autumnal aspect plants are able to out compete the grass plants and initiate a scrub stage in the succession that precedes the invasion of forest. The lack of resistance by these plants to fires prevents the succession to scrublands in the face of frequent fires. Thus, the autumnal aspect plants should require longer fire intervals than the vernal aspect plants to exist in a sward (Bayer 1955).

Grass plants are structured such that they are able to tolerate defoliation by fire (Tainton & Mentis 1984). This is achieved by maintaining the meristematic apex of the grass stem close to the soil surface during vegetative development. This way defoliation is limited to the removal of only the mature and young leaves and the dry matter during the vegetative development stage (Burgess 1991). At some point in their development, most tillers of grass species switch from vegetative to reproductive growth. This terminates the vegetative leaf-producing stage and is usually accompanied by a rapid elongation of the internodes of the stem. The meristematic and now reproductive apex is elevated to the degree that it is extremely vulnerable to any form of defoliation. However, the removal of the reproductive apex at this stage will only prevent the formation of flowers and seed. This is because its removal is usually accompanied by the development of the next generation of tillers from basal stem node positions, at least in perennial plants (Tainton & Mentis 1984). In this respect, bunch grass and sod-forming species are affected differently by fire (Dillon 1979). The nodes from which tillers develop in the bunch grass species (e.g. *Themeda triandra*) are normally borne above the soil surface, whereas those of the sod-forming species (e.g. *Tristachya* *leucothrix*) are normally borne at or below the soil surface (Everson, Everson & Tainton 1988). This suggests that sod-forming species would be more resistant to frequent and intense defoliation than bunch grass species (Tainton & Mentis 1984). However in the field bunch grasses are found to dominate frequently burnt areas, whereas the sod-forming species dominate infrequently burnt grassland (Everson & Tainton 1984). This seems to arise from the inability of the bunch grasses to survive where the canopy remains dense for any length of time (Tainton & Mentis 1984). New tillers of these bunch grass species will not develop from heavily shaded basal nodes, but will develop from elevated positions. These elevated tillers do not develop effective roots and die before reaching maturity. In contrast, sod-forming species that produce tillers from initials borne at or below the soil surface are relatively unaffected by dense base shading (Everson, Everson & Tainton 1988).

1.7 AIMS OF THIS STUDY

There has been considerable research into the effects of fire on grassland vegetation in southern Africa. However, most of this research has had an agricultural focus on the grazeable component of the sward. This has provided good insights into the effect that various fire regimes have on grass species, but few other taxa have received any attention. The forb component, which has largely been ignored, constitutes most of the botanical wealth of the grasslands, including many rare and endangered species of interest to conservation. Thus, little is know about how fire regimes affect species diversity in southern African grasslands. This means that the effect of the primary grassland management tool, on diversity, is inadequately understood. The aim of this project was thus to examine how various fire regimes influence the diversity of the entire vegetation community and to explore ways of maximising this diversity.

THIS STUDY:

To address this problem, the effect of different burning treatments on species composition and richness was examined in three different long term burning trials in South Africa. Located in the fire climax grasslands east of the escarpment, these trials consisted of a range of treatments randomly allocated to plots in a replicated block design. Manipulated according to frequency and season, burn treatments were sampled to examine the effect of different fire regimes on alpha diversity (at $1m^2$ & $100m^2$) at each site and beta diversity across the catchments at Cathedral Peak. Further, the effects of frequency and season of burn were examined on a range of sward attributes.

THE EFFECT OF FREQUENCY AND SEASON OF BURN ON SPECIES DIVERSITY:

Fire is one of the primary management tools used in the grassland biome. In particular, its manipulation is important in conservation areas where grazing mammal densities are usually low. Therefore to conserve the floral wealth of this biome, it is necessary to understand how different burning regimes affect species diversity. As discussed in Chapter 1.2, the simplest measure of diversity is species richness. Related to this, is the division of species between the replicates of each treatment and between the treatments at the site. However, species are seldom equally abundant at a site. Where species occur in small populations and/or restricted geographical areas or habitats, they are considered to be at risk of extinction (Rosenzweig 1995). Due to the possible local extinction of the less common species at a site, it is important to explore which burning regimes may favour these species.

When considering the species diversity of an area, it is just as important to consider the evenness of the species as the species richness. In this regard, it was necessary to examine the effect that fire has on evenness. To achieve this, the factors that influence the presence and distribution of species across the treatments were examined using ordination techniques. This was done using the abundance of species in each treatment.

THE INTERMEDIATE DISTURBANCE HYPOTHESIS AND DIVERSITY PATTERNS IN THE GRASSLAND BIOME:

Though definitions of disturbance vary, they all indicate that disturbance is the product of factors, external to the hierarchical level of the system, which cause change in the system (Pickett, Kolasa, Armesto & Collins 1989). Two forms of disturbance may then be identified: direct disturbances affect the survivorship of individuals directly; conversely, indirect disturbances affect the resource levels or other conditions that then influence individuals in a patch (Hobbs & Huenneke 1992). Fire qualifies as both a direct and indirect disturbance influencing vegetation patterns (Bond 1997). The effect fire has on a system depends on a number of factors including: the frequency, season, intensity, duration and area of burn (Bond & van Wilgen 1996). It is therefore possible to use these various factors to examine the role of disturbance in maintaining species diversity in the grassland biome.

Early observations from intertidal (Paine 1966; Sousa 1979), coral reef (Connell 1978) and forest (Eggeling 1947; Connell 1978) habitats suggested that species diversity was highest at intermediate levels of disturbance (Petratis, Latham & Niesenbaum 1989). At very high rates of disturbance it was predicted that only those species tolerant of these extremes might survive. Alternatively, at very low rates of disturbance, there would be sufficient time for competitive exclusion to reduce the number of species (Bond & van Wilgen 1996). Diversity would then be highest in communities with moderate levels of disturbance and at intermediate time spans following disturbance (Connell 1978; Grime 1979; Huston 1979; Collins, Glen & Gibson 1995). Much of the experimental evidence for the intermediate disturbance hypothesis (IDH) (Connell 1978; Huston 1979) has come from systems with high growth rates and high rates of competitive displacement (Huston 1994; Bond & van Wilgen 1996). But, does the IDH apply to other communities, especially those where fire is the disturbance and in particular, does it apply to grasslands?

Studies from fire-prone systems have not unanimously supported the IDH. Work done in the Scottish heathlands showed an increase in the number of species with increasing fire frequency (Hobbs, Mallik & Giningham 1984). This suggested that the highest species diversity is to be achieved by frequent burning. However, there were no stands burnt at intervals shorter than six years, so the predictions of the IDH were only half tested. Conversely, studies from the North American tallgrass prairie (Collins & Gibson 1990; Collins, Glenn & Gibson 1995) showed a decrease in the number of species with increasing fire frequency. However, these studies also showed that the number of species reached a maximum at an intermediate time interval since the last disturbance, thus half fulfilling the predictions of the IDH (Collins, Glenn & Gibson 1995). Studies from another fire-prone system, the South African fynbos (Schwilk, Keeley & Bond 1997), found the number of species, at most spatial scales, to be lowest at intermediate fire frequencies. In the smallest plots sampled (1m^2), species diversity increased with increasing fire frequency. This matched the pattern found in the Scottish heathlands where sampling was also done using 1m^2 quadrats (Hobbs *et al.* 1984). When species diversity in the fynbos was sampled at larger spatial scales (100 - 1000m^2) there was an inverse pattern to that predicted by the IDH. Schwilk *et* *al.* (1997) explain this discrepancy in species diversity trends between small and large plots as possibly being an artefact of plot size. They suggest that frequent fires select for small plants. As Oksanen (1996) observes, the smaller the individuals, the more individuals and species that can occur in a plot. As plant size increases (which Schwilk *et al.* (1997) suggest will be a factor of increasing interval between burns), fewer individuals can occur in the same sized plot, so decreasing the potential species diversity. However, at larger spatial scales, the effect of decreased habitat heterogeneity with increasing fire frequency may cancel this effect of plant size (Schwilk *et al.* 1997).

HETEROGENEITY AND THE EFFECT OF FREQUENCY AND SEASON OF BURN:

Conclusions regarding species diversity are dependent on the scale of measurement. Of two sites, one may have a higher species diversity at a point scale of 1m^2, while the other may have a higher species diversity in 1000m^2. This occurs because species accumulate at different rates as sample area increases at each site (Schwilk *et al.* 1997). As Rosenzweig (1995) observes, most species only occur in the presence of a particular set of habitats. Therefore, as the number of available habitats increases, the potential to include more species grows. The larger the area being sampled, the greater number of habitats, and potentially the number of species that can be contained within it. By plotting the rate at which species accrue with increasing area (the slope of the species/area curve), heterogeneity may be compared between communities (Whittaker 1977; Bond 1983). The steeper the slope of the species/area curve, the greater the heterogeneity as the number of habitats, and therefore species, accrue at a faster rate as area increases. Community heterogeneity may also be measured by comparing the mean degree of dissimilarity in species composition among multiple points in the community (Collins 1992). Because disturbance creates spatial heterogeneity within communities (Schwilk *et al.* 1997), it is possible to examine the effect of different fire regimes on community heterogeneity and thus species diversity.

THE EFFECT OF FREQUENCY AND SEASON OF BURN ON A RANGE OF SWARD ATTRIBUTES:

PERCENTAGE COVER:

The percentage canopy cover of a sward is not only important for grazing but also plays a role in preventing erosive soil losses (Everson, George & Schulze 1989). As with much grassland research, measures of percentage cover have long had an agricultural focus, largely ignoring the non-grazeable component of the sward. However, to fulfill conservation goals it is important to examine all the species. In the species-rich grasslands studied, most of the forb species constituted very little of the aerial cover. It was thus only practical to examine how the cover of dominant species were affected by different burning regimes.

LIGHT ATTENUATION:

The competitive ability of plants in a sward is determined by the correlation between the set of life history and physiological characteristics of that plant (Huston & Smith 1987). These correlations result from physiological and energetic constraints on the capture and use of, among other resources, photosynthetically active radiation (Smith & Huston 1989). The amount of photosynthetically active radiation available to each species will be determined by its height in relation to the height and density of the sward canopy. Therefore, the species which dominated the aerial cover of each plot will define the dimensions of the sward canopy. Where species are shorter than the sward canopy, their presence will be subject to their light requirements and the density of the sward. Therefore, if different burning regimes affect the height and density of the sward canopy, they may also explain sward composition. The effect of fire on sward structure was thus examined by using the amount of light filtered out by the sward to calculate the average cumulative total leaf area per unit ground area at 100mm intervals down the sward. This served as a measure of the relative density at each level sampled down the sward.

BIOMASS:

The effect of fire on sward structure was also explored by examining how different burning regimes affected the biomass of the sward. Biomass is the product of both sward height and density and thus mostly represented by the species dominating the aerial cover of the plots. Grasses therefore constituted most of the biomass, making this measure of interest to both the conservationist and grazier.

BIOMASS AND SPECIES RICHNESS:

A number of authors have demonstrated a hump-backed relationship between biomass and the number of species in herbaceous communities (Al-Mufti, Sydes, Fumess, Grime & Band 1977; Grime 1979; Wheeler & Giller 1982; Bond 1983; Moore & Keddy 1989; Wisheu & Keddy 1989; Wheeler & Shaw 1991; Wilson & Shay 1990; Garcia, Mararion, Moreno & Clemente 1993; Rosenzweig & Abramsky 1993; Abrams 1995) If such a hump-backed relationship exists for the southern African grasslands, it may be possible to predict the species richness of a site based on its biomass. O'Connor & Bredenkamp (1997) have shown that biomass in the grassland biome is related to rainfall in a linear fashion. Therefore, the possibility exists to predict species richness based on the rainfall an area receives. Knowing how sites of different biomass respond to various burning treatments would then allow managers to predict burning strategies to maximise species diversity for that site.

APPROACH:

The burning trials sampled for my study were used to examine the effects of frequency and season of burn on phytodiversity. This was done at different scales using a variety of measures. One of these measures, species richness, was then used to examine whether diversity peaked at intermediate levels of disturbance and thus supported the predictions of the IDH. The effects of different burning regimes were also examined to determine whether fire could cause vegetation patchiness by influencing the species composition. Further, the effects of fire on the composition of the aerial cover, sward structure and biomass were explored as potential explanatory variables. Species richness was also related to the average biomass at each of the three sites to test for a hump-backed relationship across the grassland biome. Due to a general lack knowledge of the basic biological of the grassland forb flora, the division of taxa among families underground organs possessed by the forbs were examined at each site. The three sites examined in my study are reported on in the order they were sampled.

KWAZULU-NATAL MIDLANDS

2.1 INTRODUCTION

The KwaZulu-Natal Midlands represent a region of intermediate rainfall, relative to the other two sites. Here, in the absence of fire or an alternative defoliation agent, a community of tall grasses, vernal aspect forbs and dwarf shrubs develops. In the continued absence of defoliation, the tall grasslands are replaced by a community of scattered trees, in a sparse moribund sward. Frequent burning promotes a dense, medium grass sward, dominated by the preferred grazing species, *Themeda triandra*. These grasslands have long been a centre of grassland research, with a variety of burning trials providing a considerable portion of the southern African grassland literature. A large degree of what we know about the effects of different burning regimes on the composition and productivity of grass swards has come out of these trials (Tainton & Mentis 1984). Unfortunately, the trials in the KwaZulu-Natal Midlands at Cedara, Estcourt, Nottingham Road, Tabamhlope and Underberg are no longer in existence, making the burning/mowing trial at Ukulinga the only long-term defoliation trial that is currently being maintained in the region. The effects of frequency and season of burn on various aspects of phytodiversity were sampled in this trial, using a variety of methods. These diversity measures were then used to test the intermediate disturbance hypothesis and the effect of different burning regimes on vegetation patchiness. In addition, the response of a range of sward attributes (sward composition, structure and biomass) to the burning treatments, were also examined.

2.2 SITE DESCRIPTION

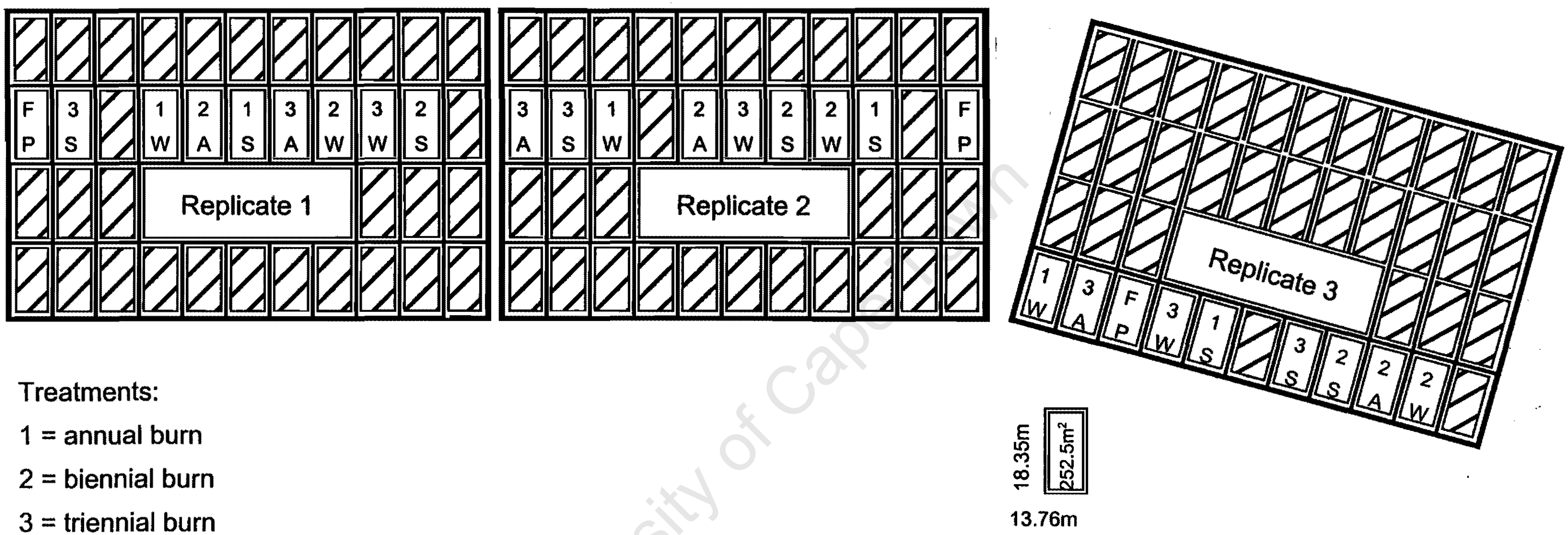
The study site is located at Ukulinga, the University of Natal's research farm (29°40'S 30°24'E), situated eight kilometers south-east of Pietermaritzburg in

KwaZulu-Natal, South Africa (Figure 1.1). The burning/mowing trial is maintained by the Department of Range and Forage Resources. Started in 1950, the trial was initiated to monitor the effects of burning and mowing treatments on spring recovery growth, herbage quality, and the development quality of individual tillers of the grass *T. triandra* (Tainton, Groves & Nash 1977).

Ukulinga is situated on a plateau in undulating hilly terrain, approximately 840m above sea level, receiving 735mm mean annual precipitation. The trial is located between Short Mistbelt Grasslands (Granger & Bredenkamp 1996: Vegetation type 47) and Coast-Hinterland Bushveld (Granger 1996: Vegetation type 24). The Short Mistbelt Grasslands are dominated by *T. triandra* with other grass species such as *Eragrostis racemosa*, *Diheteropogon amplectens* and *Tristachya leucothrix* prominent. In disturbed areas of this vegetation type, the grass, *Aristida junciformis* dominates.The Coast-Hinterland Bushveld is characterised by *Acacia karoo* savanna with *A. junciformis* the dominant grass. Other grass species such as *D. amplectens*, *T. triandra* and *T. leucothrix*, also dominate in well preserved areas of this vegetation type, as is the case at Ukulinga (Granger 1996: Vegetation type 24). Except for five of the 132 plots, these three grass species, along with *Cymbopogon excavatus*, dominate the largely treeless cover in the trial. Of the five plots not dominated by these grasses, three were the replicates of the non-defoliated control treatment, where *A. junciformis* dominated the herbaceous layer under a layer of mixed tree cover (Table 2.5). The other two plots were replicates of the annual winter and triennial autumn burns located in the third block. The species composition of these two plots was dominated by *Cymbopogon validus* (a ≥2m tall grass), and corresponded to a soil change. Because the species composition was unrepresentative of the site, unless otherwise stated, these two plots were excluded from the data analysis, leaving two of the three replicates for those treatments.

The site was sampled at the peak of the summer flowering season in January and February of 1998. Treatments consist of four combinations of burning and mowing regimes, defoliated in different seasons and at different intensities (Figure 2.1). Each treatment is replicated in three plots (13.76m x 18.35m), arranged in a random block design with approximately three meters between each plot. My study focussed on the effects of different fire regimes, so sampling was limited to the 24 burnt plots and three fire protection plots that did not receive mowing as part of their treatment. Burn treatments included: biennial and triennial autumn burns applied in April/May; annual, biennial and triennial winter burns applied in the first week of August; and annual, biennial and triennial spring burns applied after the first 12.5 mm of spring rain. In addition, the control plots which had not been defoliated since the trial commenced in 1950, were also sampled. Besides the control plots, all plots at the site were mown in July of 1997. This was done in preparation for a biomass cut at the end of the following growing season, so that the effects of the treatments were not confounded by the time since last disturbance.

Burning in the trials at each site was applied by initiating a back burn on the down wind side of the plots and then igniting a head burn opposite it. Carried by the prevailing winds, the head burn would run across the plot into the slowly advancing back burn. Hot burns at Cathedral Peak were also put in with a backburn first, but were done under hot weather conditions, usually at midday when the temperatures and wind speed were high, there was low relative humidity and no dew (Everson pers. comm.). For an insight into the behaviour of experimental fires see Trollope (1999).



Treatments:

1 = annual burn

2 = biennial burn

3 = triennial burn

A = autumn burn

W = winter burn in the first week in August

S = annual spring burn after the first 15cm of spring rain

FP = fire protection

▨ Hatched plots were not sampled as their treatments were not appropriate to the aims of this study.

Figure 2.1. Layout of plots sampled from the Ukulinga burning/mowing trial.

2.3 MATERIALS AND METHODS

2.3.1 DATA COLLECTION

IMPORTANCE-SCORE METHOD:

The importance-score method (Outhred 1984; Morrison, Le Brocque & Clarke 1995) was used to sample the plots in the Ukulinga trial. This entailed the use of a series of nested concentric sub-quadrats of different sizes (Figure 2.2), located in the centre of the plot being sampled. In this instance, a semi-geometric series of seven sub-quadrats; 1m^2, 2m^2, 5m^2, 10m^2, 20m^2, 50m^2 and 100m^2 was chosen. The largest sub-quadrat was demarcated by a 10m x 10m string square, suspended a meter off the ground from four poles. Diagonal strings running from the corners of this 10m x 10m square, and joined in the centre, had coloured ribbons attached along their length to indicate the corners of the inner sub-quadrats. Sampling the inner sub-quadrats involved creating imaginary lines between similar ribbons, colour coordinated for this purpose. In this way, each sub-quadrat was searched consecutively, starting with the innermost and smallest sub-quadrat. According to the importance-score method, if a species was encountered in the first and smallest sub-quadrat, it was given the maximum score (seven), which is the same as the number of sub-quadrats. If the species was first encountered in a larger sub-quadrat, then the species was given a successively lower score, with a score of one given to species first encountered in the largest sub-quadrate. Working from the centre of the plot, the method assumed that common species should only require a small sub-quadrat to be included in the sample. As species became less abundant, larger sub-quadrats would be required for them to be recorded.

The sub-quadrats were positioned in the centre of the plot according to the placement of the first corner pole. The position of this pole in the plot was

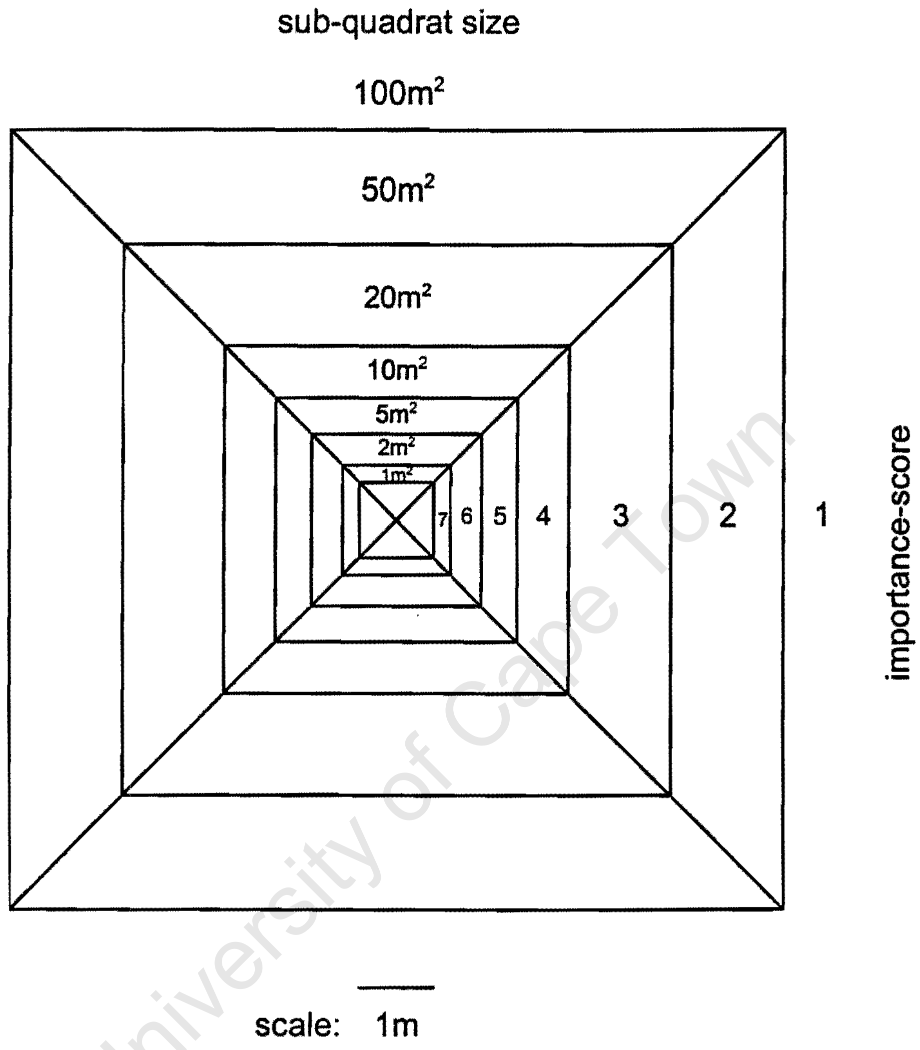


Figure 2.2. Layout of the sub-quadrats used in the importance-score method, showing the size and importance-score of each sub-quadrat and the diagonal strings used to indicate the corners of each sub-quadrat.

calculated by subtracting the width of the largest sub-quadrat (10m) from the length and breadth of the plot (18.35m x 13.76m), and halving these values. Using the values calculated in this way, the position of the first corner pole was measured from a corner of the plot. The second pole was placed by stretching one side of the quadrat parallel to the edge of the plot. The other two poles were positioned by stretching the remaining inner and outer strings such that all were straight, taut, and the diagonals (which were joined in the centre) lay at right angles to one another.

SWARD ATTRIBUTES:

PERCENTAGE COVER:

Percentage cover was taken as a visual estimate of the species that dominated the aerial cover in each plot. This was done by identifying species whose aerial cover represented five percent or more of the entire plot. These species were then allocated percentage cover estimates to the nearest five percent such that their total summed to 100 percent. As the plots were too small to adequately represent tree cover, estimates in the control plots were only made for the herbaceous layer, based on the area of the plot not covered by the tree canopy.

LIGHT ATTENUATION:

Light attenuation readings were taken in the shortest and longest spring burn intervals at each site. These readings were then used to calculate leaf area down through the sward. At Ukulinga, these were done in all replicates of the annual and triennial spring burns. Measurements of the extinction of photosynthetically active radiation (PAR) down through the sward were taken using a Decagon Sunfleck Ceptometer. Ten sets of readings per plot were made, each set starting at ground level with successive measurements taken at 100mm intervals upwards through the sward. The final reading was made at waist height above the sward (approximately one meter), representing the total incoming PAR. The number of readings made through the sward was kept constant across the replicates of each treatment, being based on the tallest area of sward in the treatment. At each 100mm interval, ten successive readings were taken and averaged using the ceptometer. The equipment was held on the horizontal using the spirit-level on the ceptometer, and each set of readings were taken with the ceptometer pointing in the same direction. To reduce the affect that the incidence of the sun may have had on the measurements, readings were taken between 11H00 and 13H00 when the sun was at its zenith, and only on cloudless days.

BIOMASS:

Biomass was sampled at Ukulinga by the UNP Department of Range and Forage Science in May 1998 at the end of the growing season, before the onset of frost. This was done by mowing a single strip (13.7m x 3.2m) to a height of approximately 70mm, across the centre of each plot, using a Falcon Haymaker lawnmower. This strip was raked and the freshly cut material weighed. A grab sample from the mown strip was taken, weighed, dried and weighed again to determine the moisture content of the sward. This was done in all plots except the control plots which were protected from any form of defoliation.

2.3.2 Data analysis

SPECIES RICHNESS:

Data recorded by the importance- score method were analysed in a variety of ways. The distribution of the numbers species across the treatments and replicates of each treatment was tabulated for comparison. The mean ($\bar{x}$) number of species (and the standard deviation, S_x) in each replicate of each treatment was expressed as a percentage of the total number of species in the treatment:

$$\bar{x} = \frac{1}{n}\sum_{i=1}^{n}\left(\frac{x_i}{y}\times\frac{100}{1}\right)$$

$$S_x = \sqrt{\sum\left(\frac{x_i}{y}\times\frac{100}{1}\right)^2 - \frac{1}{n}\left(\sum\frac{x_i}{y}\times\frac{100}{1}\right)^2 \Big/ (n-1)}$$

where: x = number of species in a replicate

y = number of species in a treatment

n = number of replicates

These $\bar{x}$ values were then compared between all treatments at the 95 percent confidence interval using the Tukey honest significant difference (HSD) general multiple analysis of variance (MANOVA) in the StatSoft Inc, STATISTICA 5.1 for windows statistical software package.

All species occurring in three or fewer plots were considered to be rare at the site. The numbers and percentages of rare species per treatment were tabulated along with their distribution across the various treatments and their replicates. Just as species richness increases with sampling intensity, so the number of rare species should increase as a proportion of the total number of species in the treatment. Based on this assumption, treatments were examined to determine whether they were supporting greater or fewer numbers of rare species than expected from their total number of species. This was achieved by linearly regressing the number of rare species in each treatment against the total number of species for that treatment using STATISTICA 5.1. Treatments that fell outside the 95 or 99 percent confidence intervals for this regressed line were considered to be having a significant effect on the proportion of rare species they contained.

ORDINATION:

Ordination is the collective term for multivariate techniques that arrange sites along axes on the basis of data on species composition (ter Braak 1988, 1995). The technique assumes a latent environmental gradient which serves to explain the species compositional gradient. In the treatments used for my study, species response to the manipulated environmental gradient at the site was considered to be unimodal. As no arch effects were observed in any of the ordinations, detrending was unnecessary and ordinations were performed using correspondence analysis (CA) and its constrained form, canonical correspondence analysis (CCA).

The aim of CA is to construct theoretical variables that best explain the distribution of species across a site. The strength of a variable is measured by the dispersion ('spread') of the species scores along the gradient created by that variable. Species score are derived from the gradient variable's average value for the sites in which the species is present. This is done to provide an optimum value for that species (the species score). The larger the dispersion of species scores, the better a variable explains the distribution of species at the site. To construct the best possible theoretical variable, the CA chooses the best values for the site, so as to maximise the dispersion of species scores. The theoretical variable constructed in this fashion is termed the first ordination axis. The second and subsequent CA axes are also constructed to maximise the species scores, but subject to the constraint that they are uncorrelated to previous CA axes. In this fashion CA extracts the ordination axes from the species data and arranges the sites on these axes. The task for the researcher is to interpret what the actual environmental variables are that are causing this dispersion of sites and species in ordination space.

Where underlying gradients are known, such as the fire frequency and season of burn manipulated in the trials sampled for my study, these may be identified and used in the ordination. Because CA extracts ordination axes from the species data alone, the effects of a particular environmental variable can not be directly analysed. The ordination axes of a CA may, however, be related to the environmental variables after extraction as a "passive" analysis of environmental variables. Where the patterns of variation in the species data need to be directly related to observed environmental variables, canonical ordinations, such as CCA, are used. A CCA offers the best fit of the environmental data supplied to the species data. This is achieved by selecting the linear combination of supplied environmental variables that maximises the dispersion of the species scores. Environmental variables are weighted and the combination of the variables that supply the best weight is used to define the first CCA axis. The second and subsequent axes are selected according to linear combinations of environmental variables that maximise the dispersion of the species scores, but subject to the constraint of being uncorrelated with previous CCA axes.

Ordination can also be applied to the variation in the community data that remains after known environmental variables have been accounted for. The ordination of this residual variation is known as partial ordination as it serves to "partial out" (eliminate) the effect of particular variables. These variables that are partialled out are called co-variables.

To test whether linear combinations of the measured environmental variables, in this case the fire treatments, had a statistically significant influence on community composition, a Monte Carlo permutation test was applied. In CANOCO 3.12 the test is applied using permutations of the residuals of the species after fitting co-variables and environmental variables. If the species react to the current environmental variables, then the test statistic calculated from the data-as-observed will be larger than most of the test statistics calculated from random data. If the observed value is among the five percent of the highest values, then the species are significantly related to the environmental variables. This may be done for the first canonical axis using its eigenvalue and as an overall test of the effect of the environmental variables on the species using the sum of all canonical eigenvalues (the trace) (ter Braak 1988, 1995).

The data collected in the Ukulinga burning trials by the importance-score method was ordinated using CANOCO 3.12 (ter Braak 1991). Importance-scores for each species were converted into percentages of the highest score and arranged in a spreadsheet format as an ASCII DOS text file. The ECOFRAME conversion program (Derry 1997) was used to prepare the data for ordination, by specifying a FORTRAN format statement for the data. Except where stated, the CANOCO 3.12 default settings were used to run ordinations and the output was displayed using CANODRAW 3.0 (Smilauer 1993). The initial ordination of the data was a CA with a passive analysis of environmental variables. The frequency and season of burn were coded as environmental variables for each site. Based on this ordination, a second CA, with a passive analysis of environmental variables, was performed without the replicates of the fire protection treatment. As the annual winter and triennial autumn burn plots in the third block of replicates differed markedly in species composition, corresponding to a soil change, their influence on the ordination was reduced by passively down weighting them and rerunning the ordination. Finally a CCA was run on the data using co-variables. A Monte Carlo test was performed at the end of this CCA using 200 random permutations. The co-variables used in the CCA were derived from the eigenvalues of the first two axes of a principal components analysis done on a range of soil variables, including: acid saturation, acidity, calcium, cations, clay content, density, depth, extractable acidity, magnesium, manganese, organic matter, phosphorus, potassium and zinc (Morris pers. comm.).

INTERMEDIATE DISTURBANCE HYPOTHESIS:

The IDH was examined in the smallest (1m^2) and largest (100m^2) sub-quadrats sampled from each treatment. The mean number of species and standard deviation, calculated from the replicates of each treatment, was graphed, according to the season of burn, against the frequency of burn using STATISTICA 5.1. These graphs were inspected for indications that species richness peaked at intermediate burning frequencies.

HETEROGENEITY:

The heterogeneity of each treatment in the Ukulinga burning trials was examined using the data collected by the importance-score method. This was done by comparing the slopes and intercepts of linearly regressed lines of the double logarithmic form of the species-area curve. These regressed lines were calculated for each treatment using of the number of species per sub-quadrat in each replicate against the area of that sub-quadrat. Linear regression was performed using STATISTICA 5.1. The slopes of these lines were compared at the 95 percent confidence interval using the algorithm for the analysis of covariance presented by Sokal and Rohlf (1995).

DISSIMILARITY COMPARISONS:

Species turnover between treatments was compared by calculating the Percentage dissimilarity (100% = most dissimilar) within and between treatments, using Releve Manager 1.08 (Cornell Ecological Programs). Within treatment dissimilarity was also examined by comparing the dissimilarity between the replicates of each treatment, to the dissimilarity between replicates of that treatment and replicates of every other treatment. This was tested by calculating the lower 95 and 99 percent confidence intervals for the dissimilarity between the replicates of the treatment being tested and the replicates of every other treatment. Where the dissimilarity within a treatment fell outside these confidence intervals, the replicates of that treatment were significantly more similar to each other than to replicates of other treatments.

SWARD ATTRIBUTES:

PERCENTAGE COVER:

Percentage cover estimates for each treatment were taken as the mean of the estimates made in the three replicates of that treatment. All species, where at least three of the treatments had percentage cover estimates greater than five percent, were graphed. Species graphs were created according to burn season as the percentage cover against burn frequency.

LIGHT ATTENUATION:

In every set of ceptometer readings, the values at each level of the sward were converted to a percentage of the total available PAR. From these percentages, a set of light attenuation values was calculated for each of the two treatments examined. This was done for each treatment by averaging, across the three replicates of the treatment, the percentage PAR at each level measured in the sward. Light attenuation was reflected according to the average cumulative total leaf area per unit ground area (F). F was calculated for each level of the sward according to the percentage PAR reaching that level. This was done using the equation:

$$F = \frac{\ln\left(\frac{J_o}{HJ_o}\right)}{k}$$

where H is the proportion of incident PAR reaching that level of the sward and k, the foliar absorption coefficient. k ranges between 0.3 and 1.3 for most leaf canopies, with a value of 0.4 in grass swards, such as the ones studied, where light easily penetrates the vertically orientated blades of the sward (Nobel 1982). J_o represents the PAR incident on the leaf canopy, and is related to F as follows:

$$\ln\frac{J_o}{J} = kF$$

where J is the photon flux density from 400 to 700nm at any level in the sward. The calculated values of F were graphed against the sward height for each burn treatment sampled.

BIOMASS:

In determining the biomass of the Ukulinga burn plots, the dry weight of the grab sample from each plot was subtracted from its fresh weight. This was done to ascertain the percentage of moisture in the sward. Based on this value, the biomass of the mown strip was calculated by subtracting the moisture content from the fresh weight of the strip. Plot biomass was then expressed in kilograms per hectare. The influence of the various burning treatments on productivity was examined at the site by graphing the biomass, according to the season of burn, against the burn frequency.

2.4 RESULTS

SPECIES RICHNESS:

Species richness showed no consistent pattern according to either the frequency or season of burn (Table 2.1). On average, each treatment only contained half the species compliment of the site, indicating the presence of species turnover between treatments. Across all treatments, the majority of species only occurred in one replicate of the treatment. The mean number of species per replicate, expressed as a percentage of the total number of species in a treatment was, on average, slightly greater than 60 percent, but did not differ significantly between treatments (*P* >0.05).

Based on the criterion that any species occurring in three or less plots at the site was considered rare, 63 of the 141 species (45 percent) recorded at Ukulinga were rare (Table 2.2). The fire protection treatment had more than double the proportion of rare species found in any of the burnt treatments (Table 2.2). Of the 27 rare species recorded in the fire protection treatment, 20 were unique to this treatment. This contrasted with the burnt treatments where more rare species were shared with other treatments than were unique to a particular treatment. Besides a single rare species that occurred in all three replicates of the triennial spring burn, the remaining rare species only occurred in one replicate of each of the burnt treatments. The fire protection treatment, however, had close to half its rare species occurring in two or more of its replicates.

ORDINATION:

In the first ordination done on the species abundance data, replicates of the fire protection treatment separated along the first axis (horizontal axis) of the CA from the burn treatments (Figure 2.3). When the CA was rerun with only

Table 2.1. Species richness of the various treatments sampled from the Ukulinga burning/mowing trial. Species were sampled from a 100m^2 quadrat in each of the three replicates per treatment; x = number of species in a replicate; y = total number of species in a treatment; z = total number of species at the site (141); n = number of replicates per treatment (3); $\bar{x}$ = mean percentage; S_x = percentage standard deviation.

	2y Aut	3y Aut	1y Win	2y Win	3y Win	1y Spr	2y Spr	3y Spr	FP
y	73	78	79	62	64	75	70	77	74
$\frac{y}{z} \times \frac{100}{1}$	51.8	55.3	56	44	45.4	53.2	49.6	54.6	52.5
Percentage of species in each treatment:									
occurring in one replicate.	44	47	43	39	45	43	46	50	46
occurring in two replicates.	33	23	30	32	27	40	30	23	27
occurring in all three replicates.	23	30	27	29	28	17	24	27	27
$\bar{X} = \frac{1}{n}\sum_{i=1}^{n}\left(\frac{xi}{y} \times \frac{100}{1}\right)$	60.7	63.7	62.5	63.4	60.9	58.2	60.5	59.3	60.4
$S_X = \sqrt{\Sigma\left(\frac{xi}{y} \times \frac{100}{1}\right)^2 - \frac{1}{n}\left(\Sigma\frac{xi}{y} \times \frac{100}{1}\right)^2 \Big/ (n-1)}$	10.6	5.2	9.2	6.5	5.4	15.0	4.1	5.2	7.8
(P >0.05 between all treatments).									

Table 2.2. Treatment effects on rare species (species occurring in ≤ three plots) in the Ukulinga burning/mowing trial. The number of rare species recorded for the fire protection treatment was significantly higher (at the 99 percent confidence interval) than what was expected according to the linear regression of the number of rare species against the total number of species recorded for each treatment.

	2y Aut	3y Aut	1y Win	2y Win	3y Win	1y Spr	2y Spr	3y Spr	FP
Total number of species.	73	78	79	62	64	75	70	77	74
Number of rare species.	9	10	14	3	4	8	6	10	27
Percentage of the species that are rare.	12.3	12.8	17.7	4.8	6.3	10.7	8.6	13	36.5
Number of rare species:									
only occurring in this treatment.	3	3	5	1	0	1	0	3	20
occurring in this and one other treatment.	4	4	4	1	4	5	3	5	4
occurring in this and two other treatments.	2	3	5	1	0	2	3	2	3
Number of rare species for each treatment:									
only occurring in one replicate.	9	10	14	3	4	8	6	9	15
occurring in two replicates.	0	0	0	0	0	0	0	0	9
occurring in all three replicates.	0	0	0	0	0	0	0	1	3

the burn treatments, the annual winter and triennial autumn burn replicates from the third block were present as outliers (Figure 2.4). With the two outlier plots downweighted, the subsequent CA for the burn treatments was presented as a bi-plot of sites with treatment effects (Figure 2.5). The first axis of this bi-plot showed some relation to the frequency of burn, however, treatments did not relate well to the effects of season of burn. Plots in the third block of replicates differed from the first two blocks as they were clustered together separately in the ordination (Figure 2.5). This suggested that environmental gradients across the site were having more of an influence on species composition than the frequency and season of burn.

To directly examine the effects of fire treatment on species composition, treatments were used, along with co-variables, in a CCA. The subsequent CCA showed division between the seasons of burn along the first axis with some division according to burn frequency along the second axis (Figure 2.6). Eigenvalues, are a measure of the importance of an axis, derived from the dispersion of species scores on the axis, ranging from zero to one. The higher the dispersion of species scores, the higher will be the eigenvalue and more important the ordination axis. Total inertia is the total variance in the species data, measured by the chi-squared of the sample-by species table, divided by the tables' total. The percentage variance of the species data explained by the axes was quite low for both the CA (Figure 2.5) and CCA (Figure 2.6), but more so in the latter after the effects of co-variables had been extracted. In the CCA this was attributable to the lower eigenvalues, the percentage variance of species data being the quotient of the eigenvalue and sum of all unconstrained eigenvalues. The sum of all unconstrained eigenvalues in the CCA (Figure 2.6) was less than the total inertia because 13,8 percent of the inertia had already been explained by the co-variables. Based on the sum of

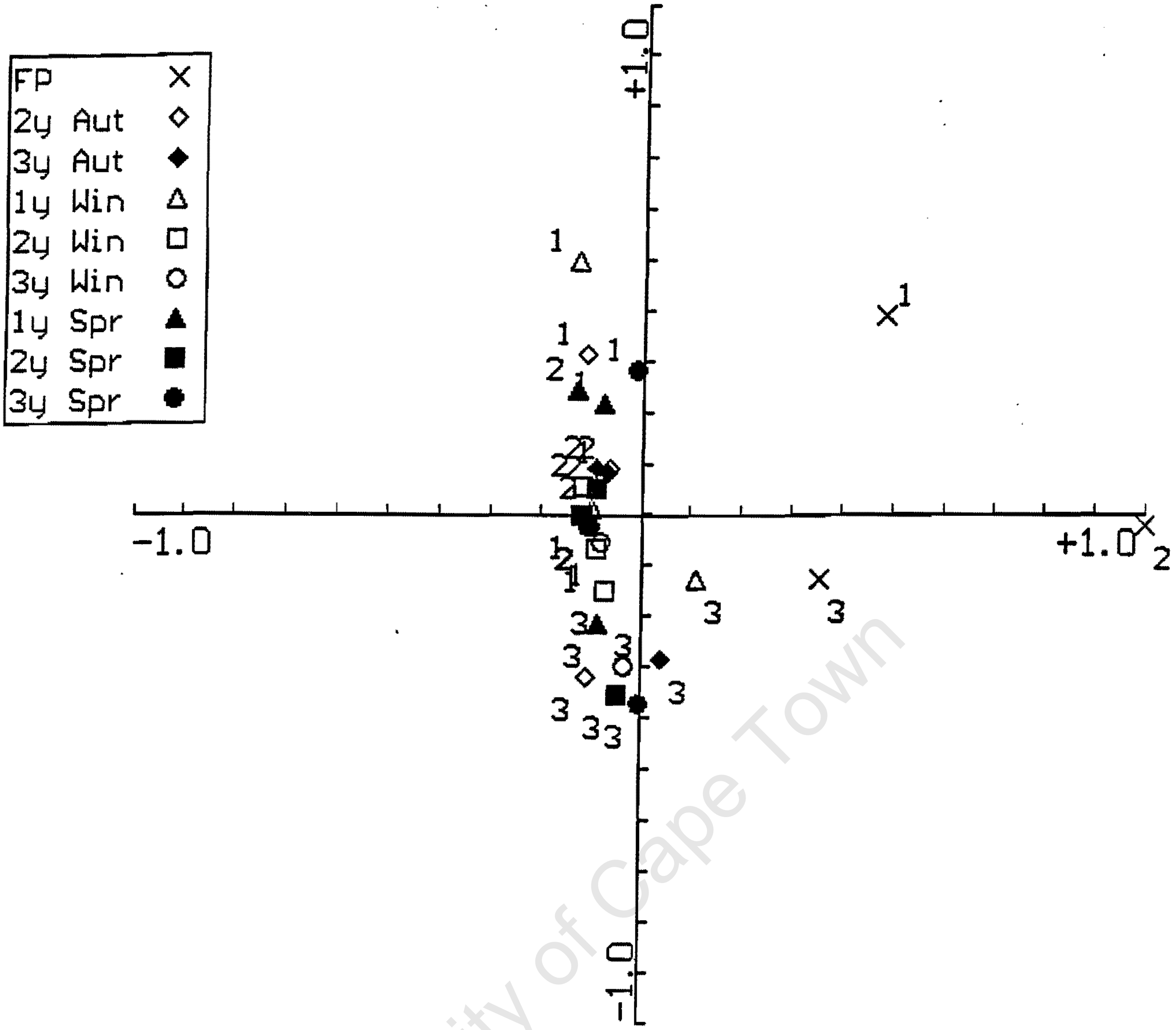


Figure 2.3. Correspondence analysis of the replicates of each treatment sampled in the Ukulinga burning/mowing trial (numbers represent blocks of replicates).

	Axis 1	Axis 2	Total inertia
Eigenvalues	0.384	0.196	2.303
Cumulative percentage of variance			
- of species data	16.7	25.2	
- of species-environment relations	55.1	59.7	
Sum of all unconstrained eigenvalues			2.303
Sum of all canonical eigenvalues			0.555

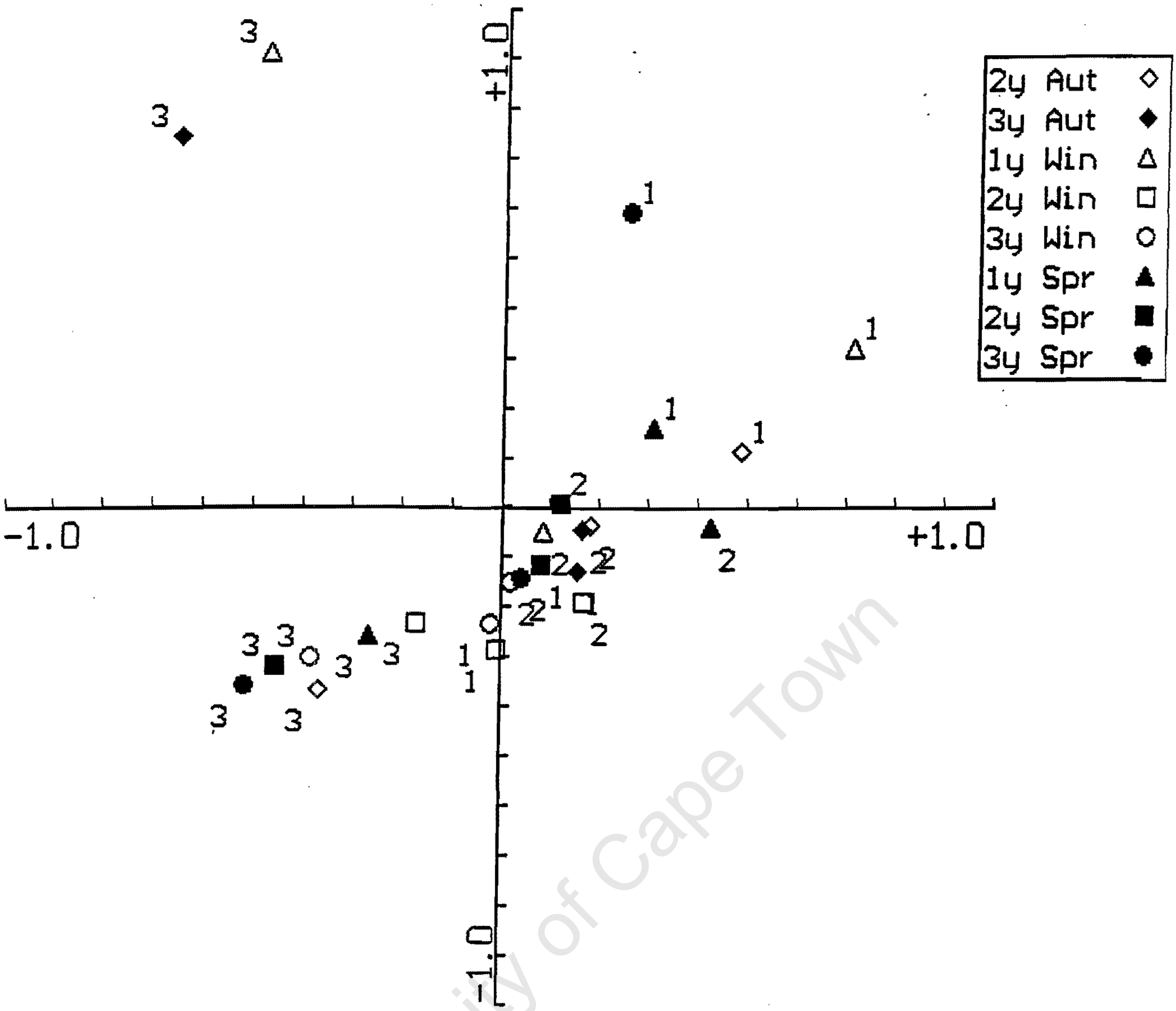


Figure 2.4. Correspondence analysis of the replicates of each burn treatment sampled in the Ukulinga burning/mowing trial (numbers represent blocks of replicates).

	Axis 1	Axis 2	Total inertia
Eigenvalues	0.206	0.182	1.790
Cumulative percentage of variance			
- of species data	11.5	21.6	
- of species-environment relations	7.5	16.0	
Sum of all unconstrained eigenvalues			1.790
Sum of all canonical eigenvalues			0.243

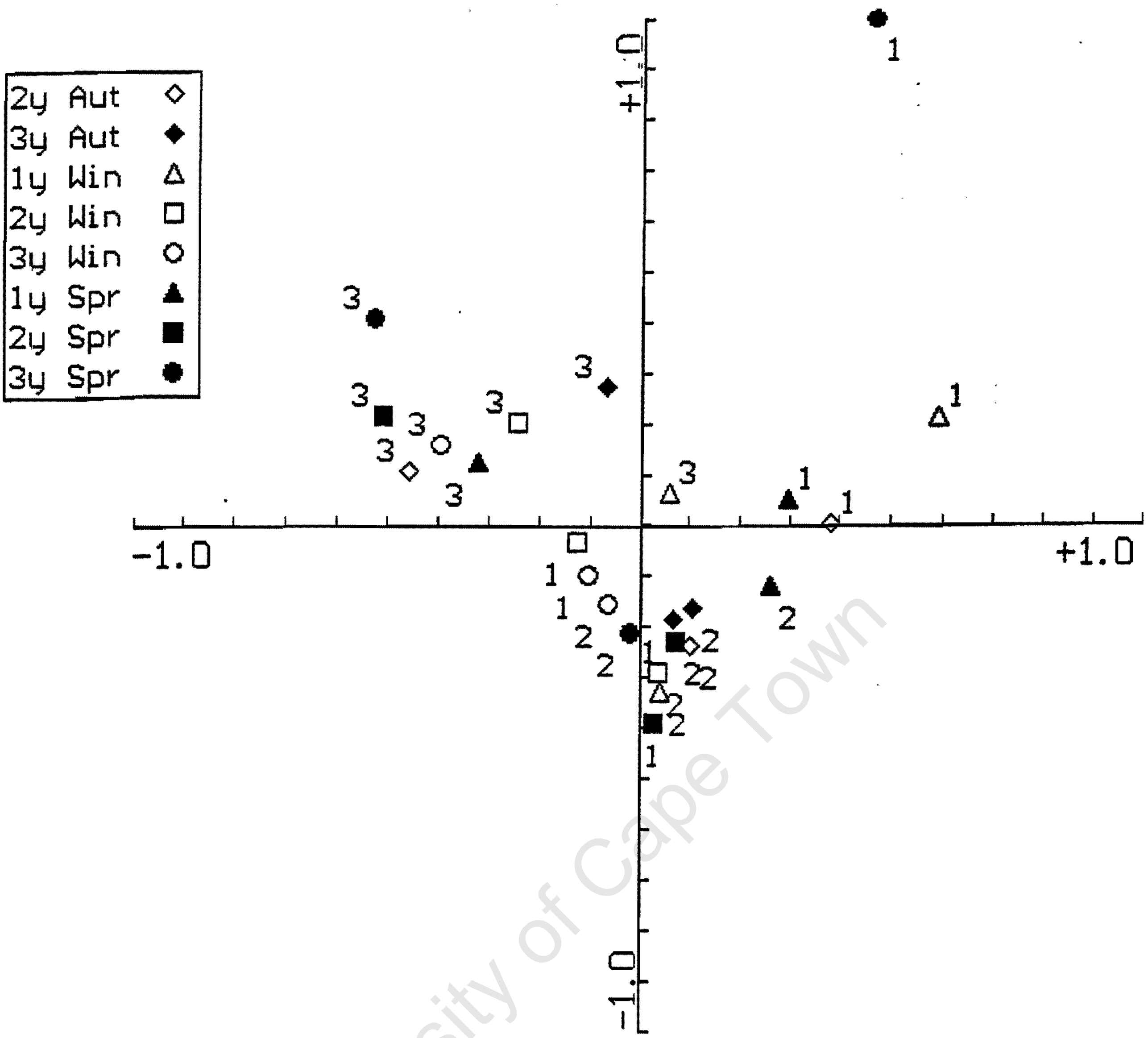


Figure 2.5. Correspondence analysis of the replicates of each burning treatment sampled in the Ukulinga burning/mowing trial, with the two outlier plots passively downweighted (numbers represent blocks of replicates).

	Axis 1	Axis 2	Total inertia
Eigenvalues	0.216	0.160	1.628
Cumulative percentage of variance			
- of species data	13.3	23.1	
- of species-environment relations	13.5	21.3	
Sum of all unconstrained eigenvalues			1.628
Sum of all canonical eigenvalues			0.252

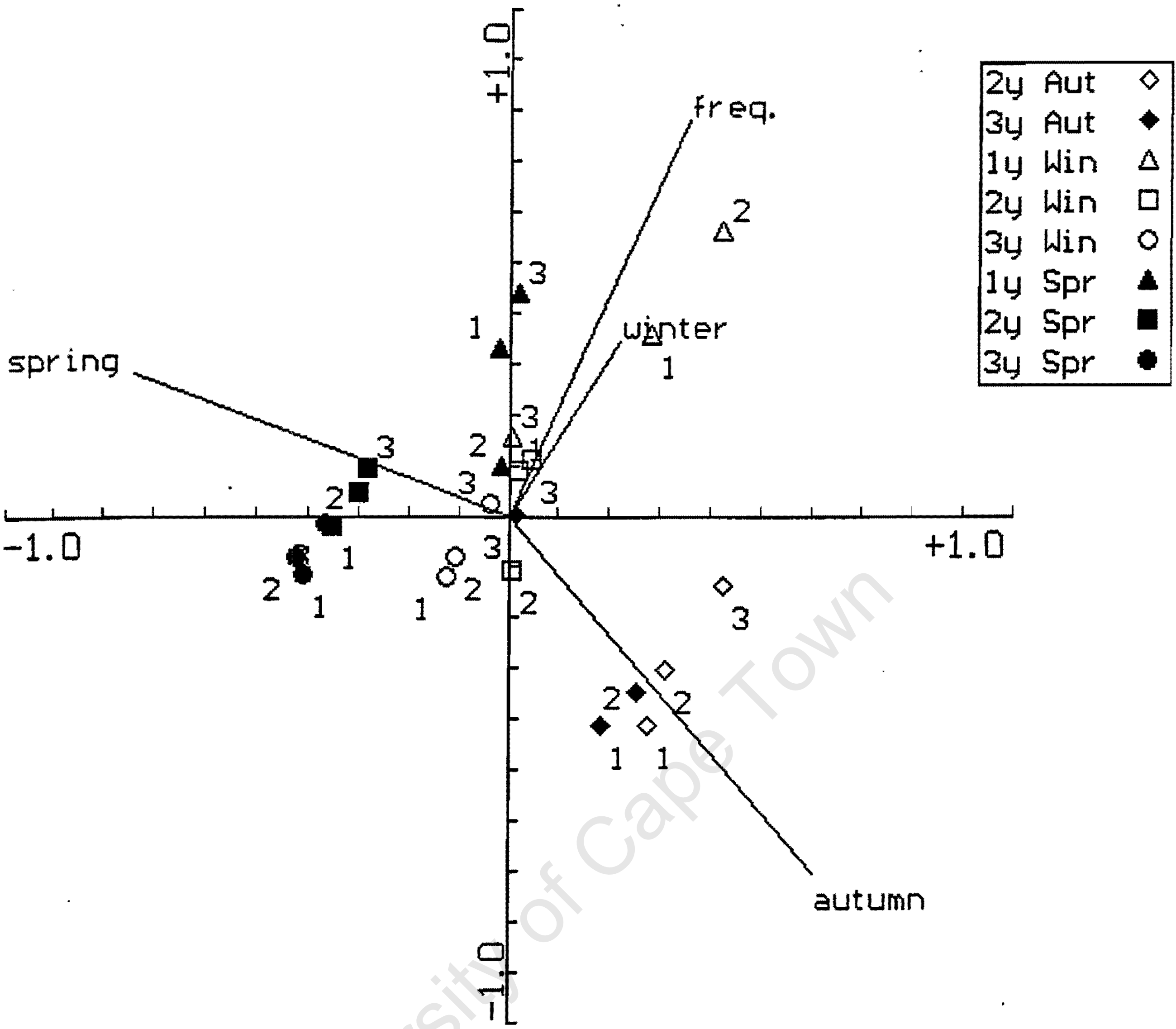


Figure 2.6. Canonical correspondence analysis of the replicates of each burning treatment sampled in the Ukulinga burning/mowing trial, analysed according to the frequency (freq.) and season of burn, with the two outlier plots passively downweighted and a Monte Carlo permutations test performed with 200 permutations (numbers represent blocks of replicates).

	Axis 1	Axis 2	Total inertia
Eigenvalues	0.096	0.082	1.628
Cumulative percentage of variance			
- of species data	6.6	12.4	
- of species-environment relations	40.2	75.3	
Sum of all unconstrained eigenvalues			1.404
Sum of all canonical eigenvalues			0.232

Monte Carlo permutation test:

	First axis	Overall test
F - ratio	1.14	1.06
P - value	0.77	0.35

all canonical eigenvalues, the current environmental variables (after fitting of the co-variables) explained 14.3 percent of the total inertia. This left 71.9 percent of the total variance in the species data unexplained.

The weak relationship between species distribution at the site and fire treatments was non-significant ($P > 0.05$) for both the first axis and the sum of all canonical eigenvalues, using the Monte Carlo permutations test. When environmental variables are included in the analysis, CANOCO uses these to explain the species data. This yields fitted values for the species. The total variance of these fitted values is the sum of all constrained (canonical) eigenvalues. Each axis explains a part of this variance, as accounted for by the percentage variance of species-environment relations. This percentage variance of species-environment relations is the quotient of the eigenvalue for that axis and sum of all canonical eigenvalues expressed as a percentage. Though the percentage variance of species-environment relations explained by the first two axes of the final CA (Figure 2.5) was low, when directly constrained by the supplied environmental variables in a CCA, the first two axes accounted for 75.3 percent of this variation (Figure 2.6). Therefore, of the 14.3 percent of the total inertia explained by the current environmental variables after fitting co-variables, 75.3 percent of this was accounted for by the first two ordination axes in the CCA (Figure 2.6).

INTERMEDIATE DISTURBANCE HYPOTHESIS:

The IDH was examined using graphs of the mean number of species per treatment at the $1m^2$ and $100m^2$ scales, plotted against the burn frequency for the different seasons. At $1m^2$, the winter burn showed a slight increase in species richness between the annual and biennial burn treatments, with species richness decreasing towards the triennial burn (Figure 2.7). Species

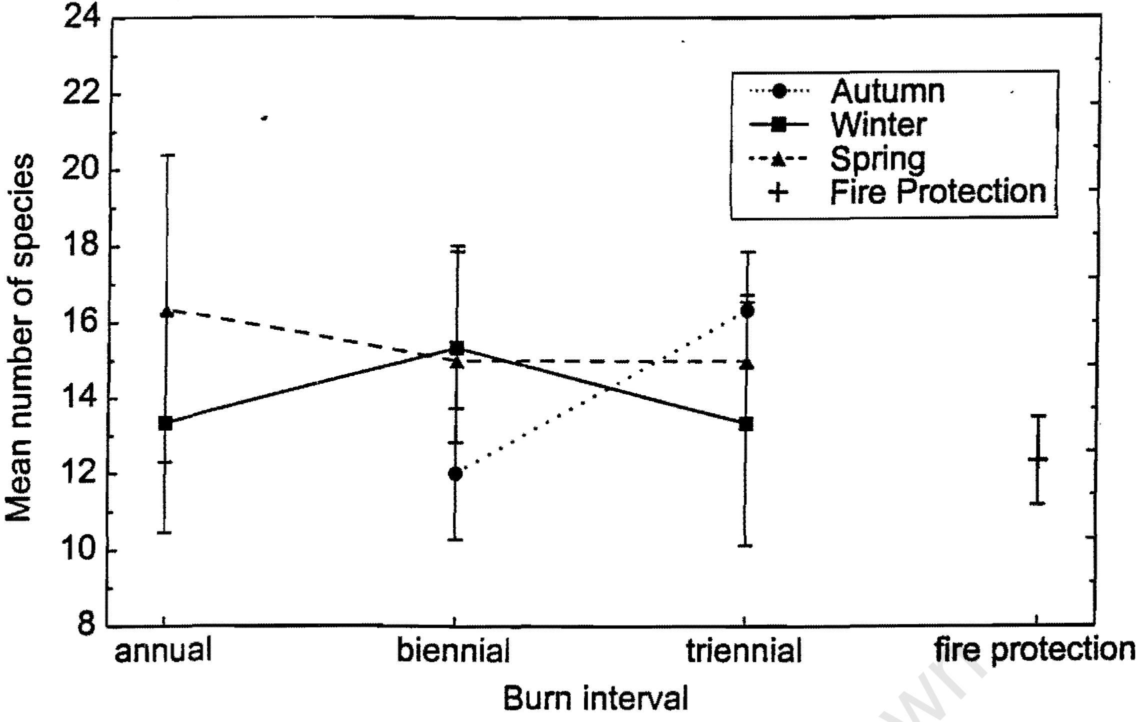


Figure 2.7. Effect of burn frequency on species richness, sampled in different seasons of burn at 1m² in the Ukulinga burning/mowing trial.

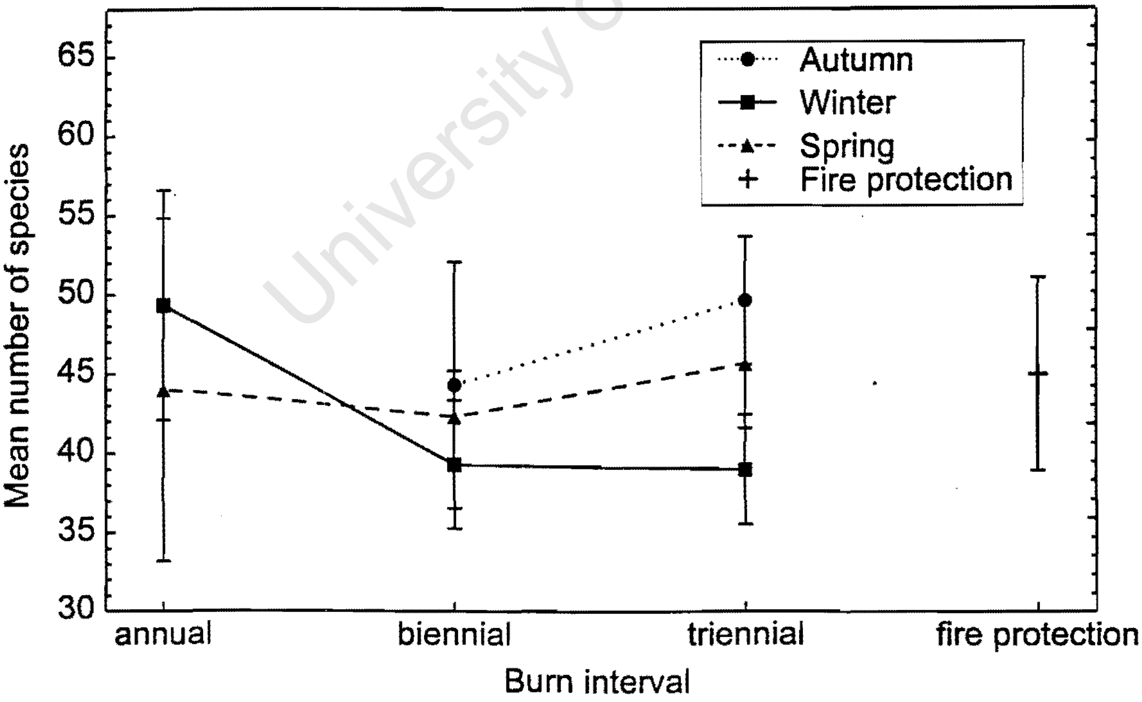


Figure 2.8. Effect of burn frequency on species richness, sampled in different seasons of burn at 100m² in the Ukulinga burning/mowing trial.

richness in the spring burn treatments did not change significantly with the frequency of burn.

At 100m^2 , the winter burn showed a decline in species richness with decreasing burn frequency (Figure 2.8). The spring burn showed a decline in species richness between the annual and biennial burns. However, like the autumn burns, there was an increase in species richness from the biennial to triennial burns (Figure 2.8). Species richness of the fire protection treatment was considerably higher than the triennial winter burn, similar to the triennial spring burn and slightly lower than the triennial autumn burn.

Of the three burn seasons, the autumn treatment was the only one that showed the same pattern between 1m^2 and 100m^2, increasing in species richness with decreasing burn frequency. Autumn burns, when compared with the fire protection treatment, were also the only treatments to peak in species richness at intermediate burn frequencies.

HETEROGENEITY:

The y-intercepts and slopes of the regressed linear relationships between the number of species and area are compared in table 2.3. The annual winter, biennial autumn and fire protection treatments produced the steepest slopes. These treatments also produced some of the lowest y-intercepts. Conversely, the annual spring and biennial winter treatments, which have the shallowest slopes possess some of the highest y-intercepts. When the slopes were compared at the 95 percent confidence interval, just over a third of the comparisons had to be excluded due to insufficient homogeneity of slope. Of the remaining comparisons, only the slopes for the fire protection and biennial winter treatments were found to be significantly different (*P* <0.05).

Table 2.3. Regression estimates for species/area curves in the Ukulinga burning/mowing trial; $y = a+bx+eps$; y = logarithm of the number of species; x = logarithm of area in m^2; a = Y-intercept; b = slope.

Burn treatments	Y-intercept	Slope	R^2
Biennial autumn	1.123	0.269	0.87
Triennial autumn	1.269	0.220	0.89
Annual winter	1.120	0.297	0.82
Biennial winter	1.197	0.209	0.91
Triennial winter	1.113	0.241	0.91
Annual spring	1.240	0.200	0.70
Biennial spring	1.161	0.232	0.82
Triennial spring	1.161	0.250	0.92
Fire Protection	1.116	0.262	0.95

DISSIMILARITY COMPARISONS:

Based on the Percentage dissimilarity within treatments, the triennial autumn, and bi- and triennial winter burn treatments produced the most homogeneous species compositions between their replicates (Table 2.4). The greatest species turnover between replicates occurred in the annual winter and spring treatments and to a lesser extent in the triennial spring and fire protection treatments. In comparisons of the dissimilarity between treatments, burn treatments were more similar to each other than they were to the fire protection treatment (Figure 2.9).

Comparing the dissimilarity between replicates of a treatment to the dissimilarity between replicates of that treatment and every other treatment, the three treatments whose replicates were the most similar (triennial autumn and bi- and triennial winter burns) (Table 2.4) were also more similar to each than to replicates of other treatments ($P < 0.01$). An exception came from the

Table 2.4. Mean Percentage dissimilarity in the species composition between replicates (sampled at 100m^2) of each treatment in the Ukulinga burning/mowing trial.

Burn treatments	Percentage dissimilarity
Biennial autumn	51.08
Triennial autumn	46.18
Annual winter	54.76
Biennial winter	47.76
Triennial winter	47.46
Annual spring	54.45
Biennial spring	51.22
Triennial spring	53.68
Fire protection	53.44

	2y Aut	3y Aut	1y Win	2y Win	3y Win	1y Spr	2y Spr	3y Spr	FP
2y Aut									
3y Aut	49.42								
1y Win	50.09	50.34							
2y Win	45.92	50.19	52.45						
3y Win	50.29	47.39	53.81	47.56					
1y Spr	47.10	52.39	51.23	45.68	52.30				
2y Spr	50.13	48.79	51.92	48.79	48.28	52.70			
3y Spr	51.22	47.85	52.23	49.81	47.27	51.38	50.38		
FP	68.81	63.36	68.41	69.37	66.35	72.27	70.44	64.15	

Figure 2.9. Percentage dissimilarity in the species composition between treatments of the Ukulinga burning/mowing trial; calculated as the mean dissimilarity between the replicates (sampled at 100m^2) of the treatments being compared.

replicates of the fire protection treatment which were also more similar to each other than to replicates of other treatments (*P* <0.01).

SWARD ATTRIBUTES:

PERCENTAGE COVER:

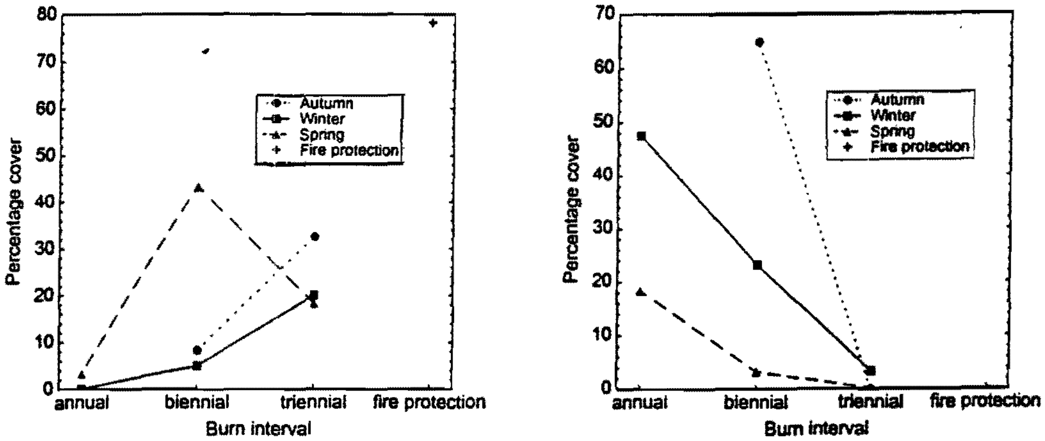
Aerial cover in the treatments sampled at Ukulinga was dominated by five grasses, *Aristida junciformis*, *Cymbopogon excavatus*, *Diheteropogon amplectens*, *Themeda triandra* and *Tristachya leucothrix* (Table 2.5). Except for the triennial spring burn, the proportion of *A. junciformis* increased with increasing interval between burns to dominate the aerial cover in the fire protection treatment (Figure 2.10). The percentage cover accounted for by *C. excavatus* increased with burn interval to its greatest representation in the triennial burns, but was less abundant in the fire protection treatment (Figure 2.10). The opposite trend was shown by *D. amplectens* (Figure 2.10) and *T. triandra* (Figure 2.10), where their cover declined as burn interval increased, to absence or minimal representation in the triennial and fire protection treatments. *Tristachya leucothrix* increased in abundance with increasing burn interval in the winter and autumn burns, but decreased under spring burning and was not recorded in the fire protection treatment (Figure 2.10).

LIGHT ATTENUATION:

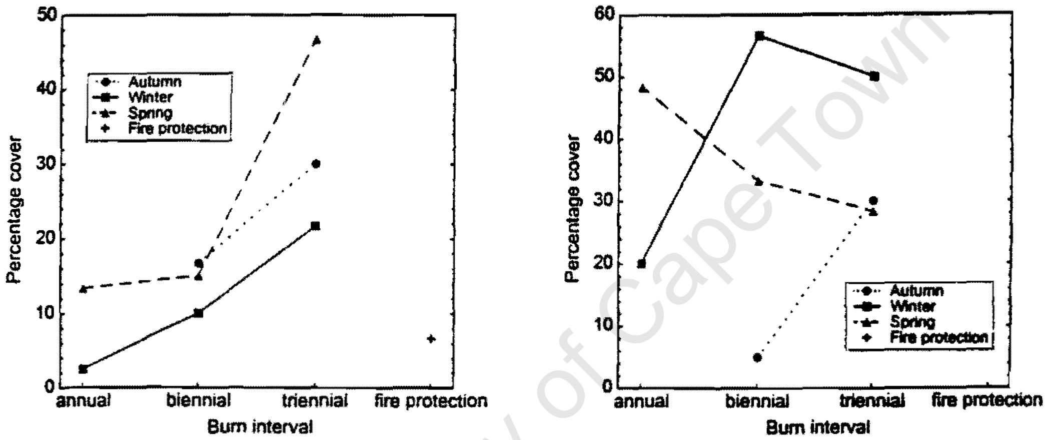
Light attenuation for the annual and triennial spring burns at Ukulinga was highest in the triennial burn (Figure 2.11). The triennial burn treatment had a taller sward and greater leaf area, as measured by the light attenuation coefficient, than the annual burn (Figure 2.11). The zero F value at the top of the sward (500mm) for the annual burn treatment indicates that the sward in this treatment did not reach this height. Examining the F down the sward, the values diverge in the middle reaches of the sward, converging again at ground

Table 2.5. Percentage cover estimates, averaged from the three replicates of each treatment in the Ukulinga burning/mowing trial.

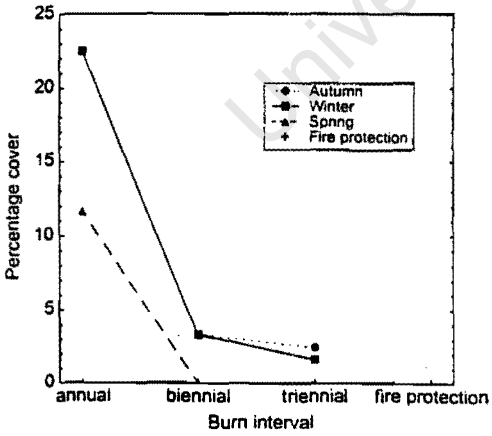
		2y Aut	3y Aut	1y Win	2y Win	3y Win	1y Spr	2y Spr	3y Spr	FP
Forbs	*Aloe maculata*	0	0	0	0	0	0	0	0	10
	Argyrolobium stipulaceum	0	0	0	0	1.7	0	0	1.7	0
	Berkheya speciosa	0	0	0	0	0	0	0	3.3	0
	Helichrysum miconiifolium	0	2.5	0	0	0	0	0	0	0
	Hypoxis colchicifolia	0	2.5	0	0	1.7	0	0	0	0
	Hypoxis hemerocallidea	0	0	0	0	0	0	0	0	3.3
	Kalanchoe rotundifolia	1.7	0	0	0	0	0	0	0	1.7
	Rhynchosia spp.	0	0	2.5	0	0	0	0	0	0
	Thunbergia atriplicifolia	0	0	2.5	0	0	0	0	0	0
Grasses	*Aristida junciformis*	8.3	32.5	0	5	20	3.3	43.3	18.3	78.3
	Cymbopogon excavatus	16.7	30	2.5	10	21.7	13.3	15	46.7	6.7
	Diheteropogon amplectens	3.3	2.5	22.5	3.3	1.67	11.7	0	0	0
	Hyparrhenia hirta	0	0	2.5	1.67	0	5	5	1.7	0
	Themeda triandra	65	0	47.5	23.3	3.33	18.3	3.3	0	0
	Tristachya leucothrix	5	30	20	56.7	50	48.3	33.3	28.3	0



Aristida junciformis *Themeda triandra*



Cymbopogon excavatus *Tristachya leucothrix*



Diheteropogon amplectens

Figure 2.10. Effect of frequency and season of burn, after 48 years of continuous treatments, on the species that dominated the aerial cover of the Ukulinga burning/mowing trial.

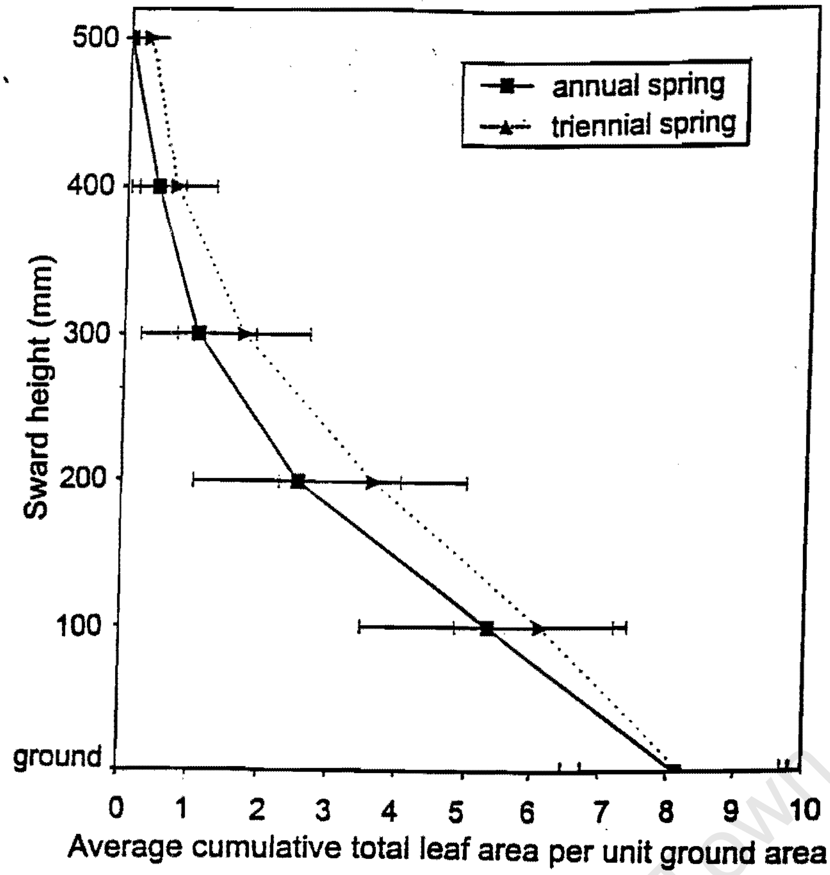


Figure 2.11. Effect of burn frequency on light attenuation down the sward in the Ukulinga burning/mowing trial, averaged from ten sets of readings in each replicate of the shortest and longest spring burn treatments.

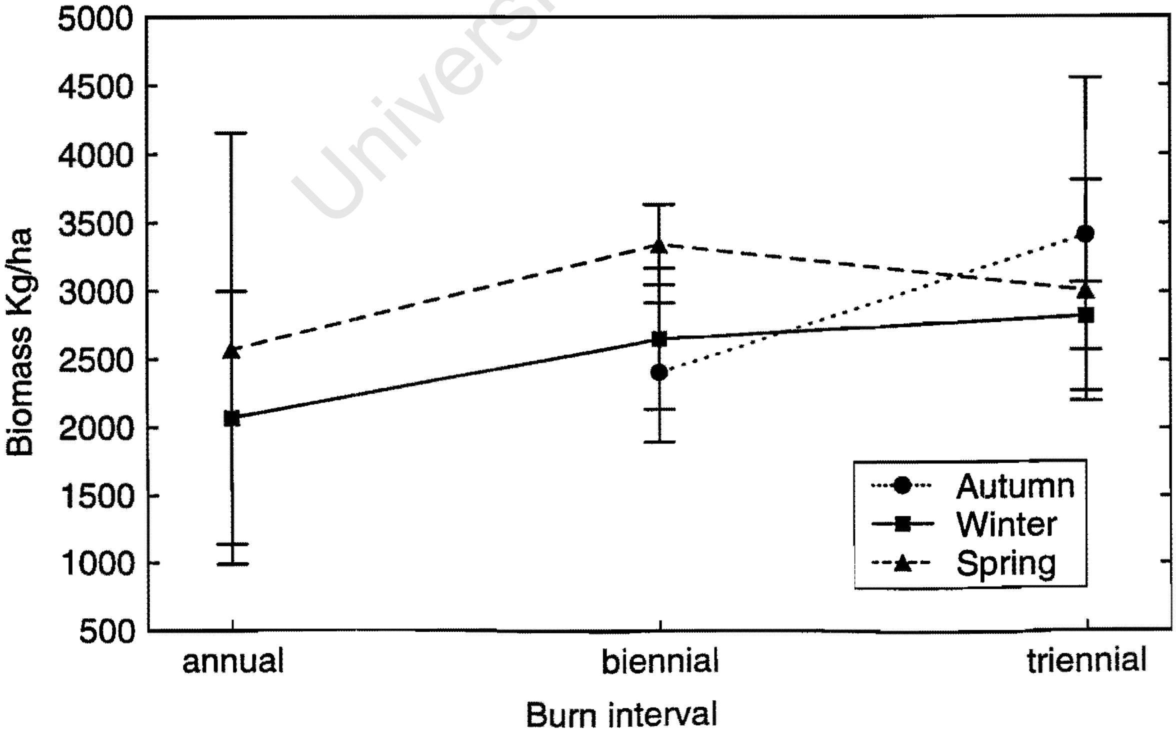


Figure 2.12. Influence of frequency and season of burn on sward biomass in the Ukulinga burning/mowing trial.

level. However, when the standard deviation around the mean is considered, the F of the two treatments did not differ significantly down through the sward.

BIOMASS:

Light extinction by the sward is related to sward biomass. Biomass decreased with increasing burn frequency for the autumn and winter burns (Figure 2.12). Biomass in the annual spring burn treatments was lower than that of the annual winter burn. The biennial spring burn, however, produced the highest biomass for any of the burn treatments at the site. Spring burning treatments also produced the highest biomass of the triennial burns.

2.5 DISCUSSION

THE EFFECT OF FREQUENCY AND SEASON OF BURN:

The questions addressed in my study revolved around the extent to which burning regimes were determining species composition and diversity patterns. For all measures of alpha diversity at $1m^2$ and $100m^2$, there was little evidence to suggest that species responded to either the frequency or season of burn. Thus, there was no support for the IDH, though there was some indication of an increase in species richness with increasing winter burn intervals (Figures 2.7 and 2.8). Measures of sward biomass showed an increase with decreasing burn frequency (Figure 2.12).

BURNING VERSUS FIRE PROTECTION:

Ordination of the species abundance data indicated that species composition differed most between the burn and fire protection treatments (Figure 2.3). This was supported by the high number of rare species only found under fire protection (Table 2.2). Dissimilarity comparisons of the species composition between treatments also suggested that burn treatments were less similar to the no burn treatment, than to each other (Figure 2.9). Unlike the burn treatments, that had been mown the year prior to sampling, the fire protection treatment had not been mown or burnt for 48 years. Thus, the differences in the species composition of the fire protection treatment may be ascribed to directional succession. After removing the effects of post burn succession, sward structure did not differ between annual and triennial spring burning (Figure 2.11).

RESPONSES TO BURNING:

Ordination results suggested that environmental gradients were having a stronger effect on the species composition of the burn treatments than frequency and season of burn (Figure 2.6). The distribution of species and rare species across the replicates of each of the burn treatments indicated that few species were being favoured by particular treatments (Tables 2.1 and 2.2). Within treatment dissimilarity measures (Table 2.4) and the proportion of the total species per treatment found in each replicate (Table 2.1) implied that frequency and season of burn were also not influencing the similarity of the species composition among replicates of each treatment. Of the nine treatments sampled at the site, replicates of only four were more similar to each other than to replicates of other treatments. The most notable of these was the no burn treatment, the rest showing no clear pattern across either frequency or season of burn. This lack of species response to frequency and season of burn explains the absence of clear trends in heterogeneity, as described by the slope of the species/area relation (Table 2.3).

Though diversity measures showed little relation to the frequency and season of burn, percentage cover of the dominant grasses responded strongly. This suggested that the sampling method used may not have been sensitive enough to record changes in forb abundance. Alternatively, changes in less abundant species, particularly the forbs, may not have been significant enough to create clear trends. The clear increase in the dominant bunch grass species and decrease in sod-forming species with increasing burn frequency agreed with work also done in the KwaZulu-Natal Midlands at Cedara and at the Estcourt and Tabamhlope Research Stations (Staples 1926, 1930; Scott 1952; Edwards 1968; le Roux 1989). Bunch grasses did better in autumn and late winter burns than in spring burning, whereas two of the three sod-forming species preferred spring burning. Similar results are reported by Tainton and Mentis (1984) from a series of trials at Nottingham Road and Underberg also in the KwaZulu-Natal Midlands. Both the effects of frequency and season of burn on the dominant grass species noted in my study were confirmed by earlier studies on the Ukulinga burning/mowing trial (Dillon 1979; Tainton & Mentis 1984).

SPECIES COMPOSITION:

One reason why the fire treatments were apparently not influencing the species composition of the plots regards the initial distribution of species across the site, and the dispersal and recruitment capabilities of the species in question. Prior to the start of the trial, species composition might have depended on the original disturbance regime applied to the site. Alternatively, species may have been distributed according to environmental gradients across the site or stochastically. Random allocation of treatments to plots would have meant that the initial species composition of their replicates would have differed. If the plants had poor distribution or recruitment capabilities, they would not be able to colonise new plots; even if the treatment applied to that plot favoured their presence. As the trial was initiated to examine the agricultural productivity of *Themeda triandra*, the initial species complement of each plot was not recorded. In addition, little is known about the dispersal and recruitment capabilities of the grassland flora. Therefore, the effect of treatments on possible trajectories of population change could not be tested.

SPECIES TURNOVER:

Pre-existing patterns may account for the species turnover between replicates and treatments. Such turnover implies that a range of treatments is needed to maintain the full complement of species at the site. Each treatment contained, on average, only half the total species recorded at the site, indicating that turnover was occurring between treatments (Table 2.1). One reason for this may have been that species differed in their response to different burning regimes (Bond and van Wilgen 1996). However, as discussed, this does not appear to have been the case. If the burn treatments had not all been mown at the same time, post-burn successional changes may have accounted for the differences in species composition. A second alternative is that species turnover between treatments may have been an artefact of species/area relations. As sample size increases, so too does the number of species (Rosenzweig 1995). Therefore as each treatment was only represented in three of the 27 plots sampled at the site, the site can be expected to have more species than any of the treatments.

SUMMARY:

Thus, fire frequencies in the range of 1 - 3 years and fire season in autumn, winter or spring had little effect on all measures of alpha diversity at 1m^2 and 100m^2, though sward biomass clearly increased with longer burn intervals. Instead, directional succession was found to result in a compositional change between the species occurring in the burn and fire protection treatments. Species occurring in the burn treatments showed a broad tolerance to the range of fire treatments. Further, environmental gradients across the site were found to have more of an impact on their composition and the structure of the sward than frequency or season of burn. The dominant grass species, however, clearly responded to the burning treatments.

EASTERN CAPE

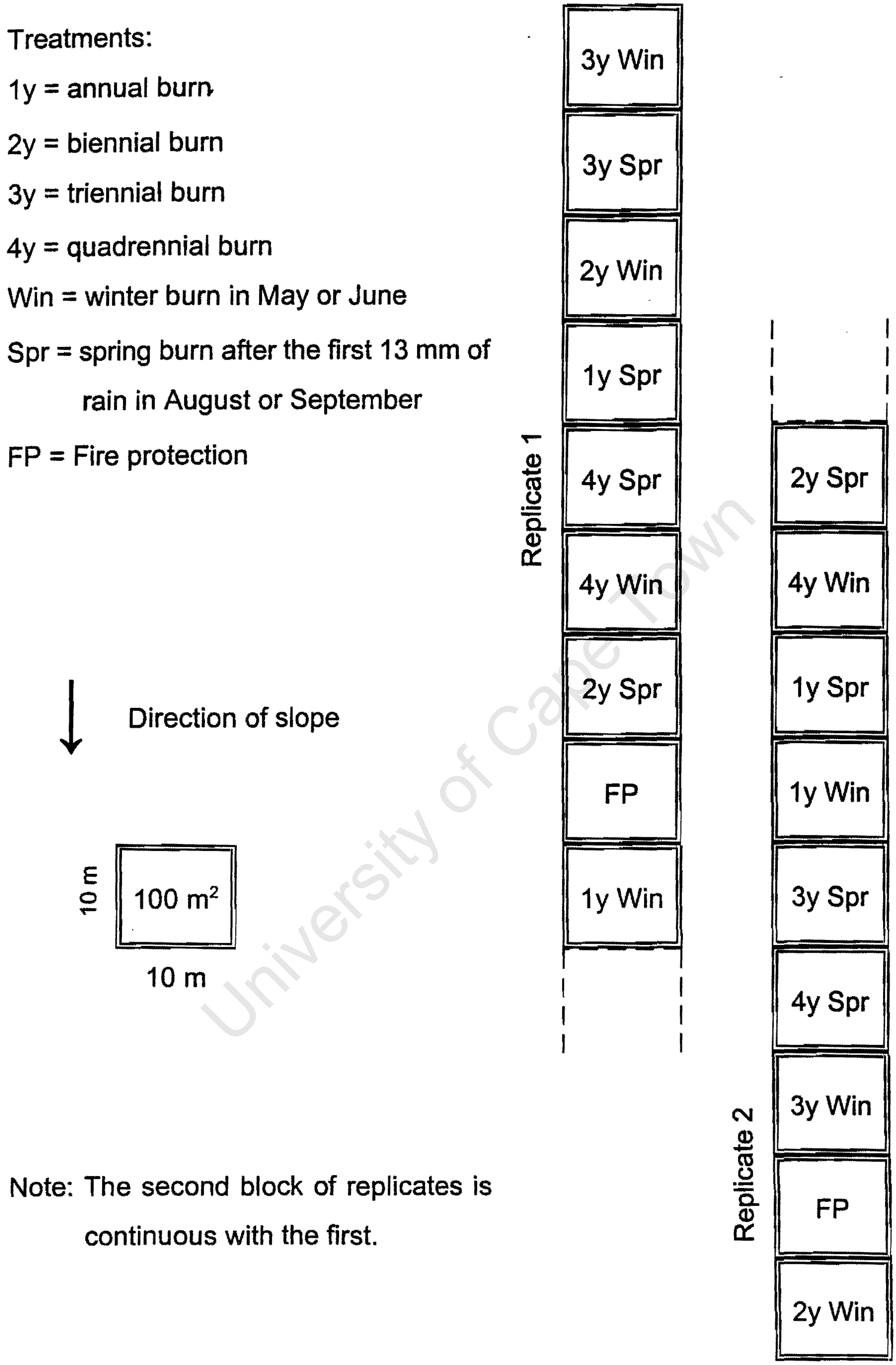
3.1 INTRODUCTION

The grasslands of the Eastern Cape occur in an area of low rainfall where frequent burning promotes medium grass swards dominated by *Themeda triandra*. With longer burn intervals, *T. triandra* is replaced by the tall, unpalatable grasses, *Cymbopogon plurinodis* and *Elyonurus argenteus* (Tainton & Mentis 1984). A significant proportion of the research in the arid grasslands of the Eastern Cape has focussed on interactions between fire and herbivory with a view to eliminating shrub species and promoting the development of grassland communities (Schonland 1927; Dyer 1932; Story 1951; Martin 1966; Trollope 1970, 1971, 1973, 1974, 1978). Much of this early work was carried out in the Amatola Mountains, with the Honeydale trials being initiated in 1973 to examine how grazeable swards could be attained using various combinations of burning and herbivory (see for example Robinson, Gibbs Russell, Trollope & Downing 1979; Trollope 1974). These trials were examined using a variety of methods to explore the effects of frequency and season of burn on various aspects of phytodiversity. The predictions of the IDH were then tested to examine ways in which phytodiversity could be maximised by manipulating the burning regime. The effects of frequency and season of burn on vegetation patchiness were also examined in both small and large plot studies. In addition, the effects of frequency and season of burn on sward composition, structure and biomass, were also examined.

3.2 SITE DESCRIPTION

Two burning trials were sampled on the Honeydale section of the University of Fort Hare's research farm (32°47'S 26°53'E), located five kilometers east of Alice in the Eastern Cape, South Africa (Figure 1.1). These burning trials are maintained by the Department of Livestock and Forage Management. Sampling on both trials was carried out in January 1999 when most forbs in the area were flowering. Situated in gently undulating terrain, around 550m above sea level, the area receives 550mm mean annual precipitation. Honeydale is located in the Eastern Thorn Bushveld (Lubke & Bredenkamp 1996: Vegetation type 16), characterised by *Acacia karoo* trees and invasive thicket species such as *Diospyros lycioides*, *Rhus* spp., *Scutia myrtina*, *Maytenus polyacantha*, and *Ehretia rigida* (Lubke & Bredenkamp 1996: Vegetation type 16). Although classified as bushveld, encroachment of woody elements can be prevented and the vegetation maintained as grassland by regular burning and browsing (Trollope 1974).

The first trial sampled was the burning demonstration treatments in camp 32 (Figure 3.1). Established in 1973 to determine the successional status of different grass species, the site was cleared of trees prior to the start of treatments (Robinson *et al.* 1979). The trial consists of nine replicated treatments, laid out in a row down a hill. Each treatment was represented by two plots (10 x 10m), randomly allocated to two blocks with approximately one meter between each plot. Treatments included annual, biennial, triennial and quadrennial winter burns done in May/June; annual, biennial, triennial and quadrennial spring burns applied after the first 13mm of rain in August/September; and a fire exclusion treatment which has not been burnt since the trial commenced in 1973. All the burn treatments last coincided in 1997 and the site was sampled in January of 1999, prior to the next biennial burn. Although *Acacia karoo* and other tree species were present in every plot except for one quadrennial spring burn, trees only dominated in the fire exclusion treatments. The aerial cover in the burning plots was dominated by two grasses, *Themeda triandra* and *Cymbopogon plurinodis* (Table 3.6).



Treatments:

1y = annual burn

2y = biennial burn

3y = triennial burn

4y = quadrennial burn

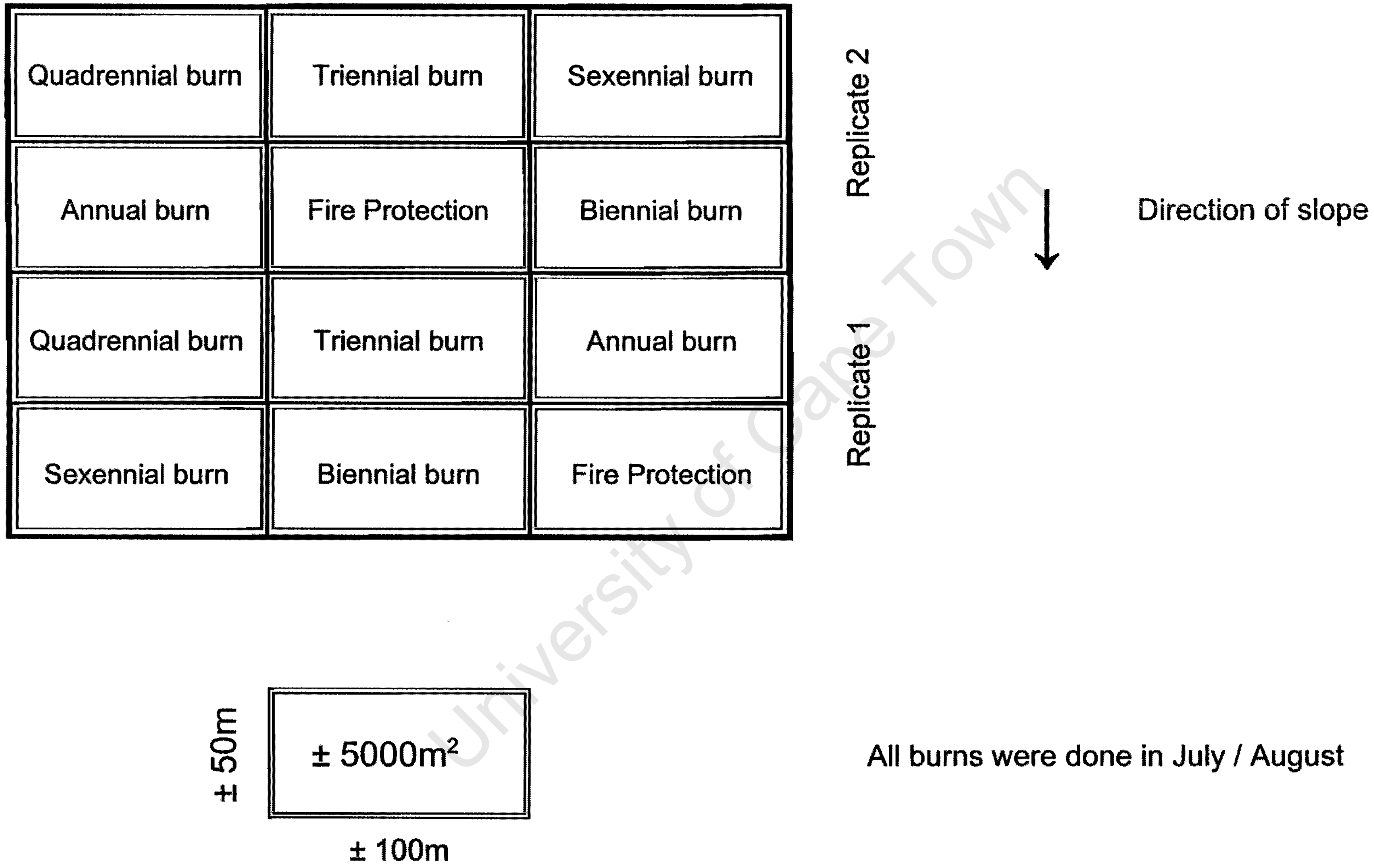
Win = winter burn in May or June

Spr = spring burn after the first 13 mm of rain in August or September

FP = Fire protection

Note: The second block of replicates is continuous with the first.

Figure 3.1. Layout of plots sampled in the Honeydale camp 32 trial.



Quadrennial burn	Triennial burn	Sexennial burn
Annual burn	Fire Protection	Biennial burn
Quadrennial burn	Triennial burn	Annual burn
Sexennial burn	Biennial burn	Fire Protection

All burns were done in July / August

Figure 3.2. Layout of plots sampled in the Honeydale camp 22 trial.

The second trial sampled was the plant succession experiment in camp 22 (Figure 3.2). Commenced in 1980, this trial was initiated to determine the successional status of grass and bush in the Eastern Thorn Bushveld. Camp 22 consists of six replicated treatments, each represented by two plots (approximately 50 x 100m), laid out in a randomly allocated block design. Treatments consist of annual, biennial, triennial, quadrennial and sexennial burns applied in winter (July/August); and a fire exclusion treatment, which had not been burnt since the trial commenced in 1980. *Acacia karoo* was present in all plots to varying extents. The sward in the fire exclusion treatments was completely dominated by the grass *Melica decumbens* . In the remaining treatments, the sward was composed of a mixture of the grasses *Cymbopogon plurinodis*, *Digitaria eriantha*, *Themeda triandra* and *Sporobolus fimbriatus*. Patches of the grass, *Panicum maximum*, were associated with the presence of termitaria, acacia trees or areas where these trees had been removed.

3.3 MATERIALS AND METHODS

3.3.1 Data collection

IMPORTANCE-SCORE METHOD:

Burning trials in camp 32 were sampled using the importance-score method (Chapter 2.3.1). Because the plots were the same size as the largest sub-quadrat used (10 x 10m), it was necessary to take into account the possibility that species close to the edge of the plot may have been introduced from outside. Thus, the origin of any new species encountered within a meter of the edge of the plot was considered with respect to those species found in the cleared area surrounding the plot. However, based on this criterion, it was not necessary to exclude any species from the samples. Also because the largest sub-quadrat was the same size as the plots being sampled, it was not necessary to calculate the position of the first pole in erecting the quadrat.

HETEROGENEITY ACROSS LARGE PLOTS:

The effects of frequency and season of burn on vegetation patchiness across large plots was sampled in the plant succession experiment (camp 32) using a two meter square quadrat. Twenty five samples were taken across the centre of each plot in a line running perpendicular to the slope of the hill. Quadrats were placed at meter intervals and the species complement of each recorded. The quadrat used, consisted of a string square with two diagonal strings running from the corners and joined in the centre of the quadrat. This structure was supported a meter off the ground by four poles. To erect the quadrat, two poles of one side were planted into the ground such that the string between them was taut. The other two poles were then moved outwards until the remaining outer and inner strings were taut and the diagonals lay at right angles to one another.

SWARD ATTRIBUTES:

PERCENTAGE COVER:

Percentage cover estimates were made in each of the burning plots in camp 32 in the same fashion as at Ukulinga (Chapter 2.3.1).

LIGHT ATTENUATION:

Ten sets of light attenuation readings were taken in each of the annual and quadrennial spring burn replicates in camp 32 in the same manner as at Ukulinga (Chapter 2.3.1).

BIOMASS:

Biomass of each plot in camp 32 was measured using a standard disc pasture meter (Bransby & Tainton 1977; Danckwerts & Trollope 1980). Fifty readings were made per plot at approximately one meter intervals. No readings were taken within a meter of the plot boundary.

3.3.2 Data analysis

Except for ordination, the data collected in camp 32 by the importance-score method; the percentage cover estimates; and the light attenuation data was all analysed in the same fashion as the data from Ukulinga (Chapter 2.3.2).

ORDINATION:

The first ordination performed on the data collected by the importance-score method was analysed using a CA with a passive analysis of environmental variables. A second CA with a passive analysis of environmental variables was run where the fire protection plots were removed from the ordination and the quadrennial winter burn in the second block of replicates passively down weighted so that the effect of the burning treatments could be further explored. Lastly, a CCA with the same modifications as the last CA was run with a Monte Carlo Test with 200 random permutations.

HETEROGENEITY ACROSS LARGE PLOTS:

The effect of fire treatments on vegetation patchiness was tested in the large burn plots of camp 22. The percentage dissimilarity was calculated and compared between treatments at the 95 percent confidence interval using the STATISTICA 5.1 Tukey HSD general MANOVA.

SWARD ATTRIBUTES:

BIOMASS:

Biomass of the treatments in camp 32 was calculated from the disc pasture meter readings using the calibration equation developed by Trollope (1983) for use in the Eastern Thorn Bushveld of the Eastern Cape :

$y = 388.3x + 340 \quad (r = 0.9126; P \leq 0.01)$

where: y = estimated standing grass crop - Kg.ha^{-1}

x = mean disc height - cm

The biomass data calculated in this way was analysed in the same manner as described for Ukulinga (Chapter 2.3.2).

3.4 RESULTS

SPECIES RICHNESS:

No clear trends in species richness were observed according to either the frequency or season of burn (Table 3.1). Though most of the spring burn treatments had more species than the winter burns, this difference only ranged between two to four species. Considered across the trial, each treatment included, on average, less than half of the total species recorded for the trial (Table 3.1). Except in the bi- and triennial spring burns and fire protection treatments, most species only occurred in one of the two replicates of each treatment. On average, the replicates of each treatment included over 70 percent of the species in the treatment, but no significant difference were found between any of the treatments ($P > 0.05$) (Table 3.1).

Of the 70 species in the various treatments, 30 (43 percent) occurred in three or less plots and were considered to be rare for the site (Table 3.2). The highest number of rare species occurred under fire protection, with six of the ten rare species being unique to this treatment. In the burn treatments most

Table 3.1. Species richness of the various treatments sampled from the Honeydale camp 32 trial. Species were sampled from a 100m^2 quadrat in each of the two replicates per treatment; x = number of species in a replicate; y = total number of species in a treatment; z = total number of species at the site (70); n = number of replicates per treatment (2); $\bar{x}$ = mean percentage; S_x = percentage standard deviation.

	1y Win	2y Win	3y Win	4y Win	1y Spr	2y Spr	3y Spr	4y Spr	FP
y	29	35	32	35	33	30	34	39	39
$\frac{y}{z} \times \frac{100}{1}$	41.4	50	45.7	50	47.1	42.9	48.6	55.7	55.7
Percentage of species in each treatment:									
occurring in one replicate.	62	60	63	57	73	47	50	62	46
occurring in both replicates.	38	40	37	43	27	53	50	38	54
$\bar{x} = \frac{1}{n}\sum_{i=1}^{n}\left(\frac{x_i}{y} \times \frac{100}{1}\right)$	69	71.4	68.8	71.4	63.6	76.7	75	69.2	76.9
$S_x = \sqrt{\sum\left(\frac{x_i}{y} \times \frac{100}{1}\right)^2 - \frac{1}{n}\left(\sum \frac{x_i}{y} \times \frac{100}{1}\right)^2 \Big/ (n-1)}$	4.9	4.0	8.8	24.2	4.3	4.7	2.1	14.5	18.1

(P >0.05 between all treatments).

Table 3.2. Treatment effects on rare species (species occurring in ≤ three plots) in the Honeydale camp 32 trial. The number of rare species recorded for the biennial winter treatment was significantly lower, and the number of rare species recorded for the annual spring and fire protection treatments significantly higher (at the 95 percent confidence interval) than what was expected according to the linear regression of the number of rare species against the total number of species recorded for each treatment.

	1y Win	2y Win	3y Win	4y Win	1y Spr	2y Spr	3y Spr	4y Spr	FP
Total number of species.	29	35	32	35	33	30	34	39	39
Number of rare species.	3	3	3	6	6	3	5	6	10
Percentage of the species that are rare.	10.3	8.6	9.4	17.1	18.2	10	14.7	15.4	25.6
Number of rare species:									
only occurring in this treatment.	2	1	1	3	2	1	0	3	6
occurring in this and one other treatment.	1	1	1	1	4	2	2	0	2
occurring in this and two other treatments.	0	1	1	2	0	0	3	3	2
Number of rare species for each treatment:									
only occurring in one replicate.	3	3	3	6	5	3	5	6	5
occurring in both replicates.	0	0	0	0	1	0	0	0	5

of the rare species recorded for a treatment only occurred in one replicate of that treatment and many were shared between treatments. However, in the fire protection treatment, half of the rare species occurred in both replicates of the treatment.

ORDINATION:

Correspondence analysis with a passive analysis of environmental variables, was performed on the frequency data collected at Honeydale. In the first CA, burn treatments were clustered together, with the two replicates of the fire protection treatment positioned separately along the first axis (Figure 3.3). The second replicate of the quadrennial winter burn treatment also separated out from the rest of the burn treatments but was considered an outlier. When just the burn treatments were examined with this outlier site down weighted, the resulting ordination showed no obvious trends according to the season or frequency of burn (Figure 3.4).

Constrained by burn frequency and season, using a CCA, treatments separated out according to the frequency of burn on the first axis and the season of burn on the second axis (Figure 3.5). The single exception to this pattern was the outlier site. Frequency and season of burn, however, only accounted for 14.5 percent of the total variance (Figure 3.5). The Monte Carlo permutation test performed on the CCA further showed that neither the first axis nor the overall test of the sum of all canonical ordination values were statistically significant ($P > 0.05$). Thus, frequency and season of burn were not found to have a marked influence on the species composition of the burn treatments.

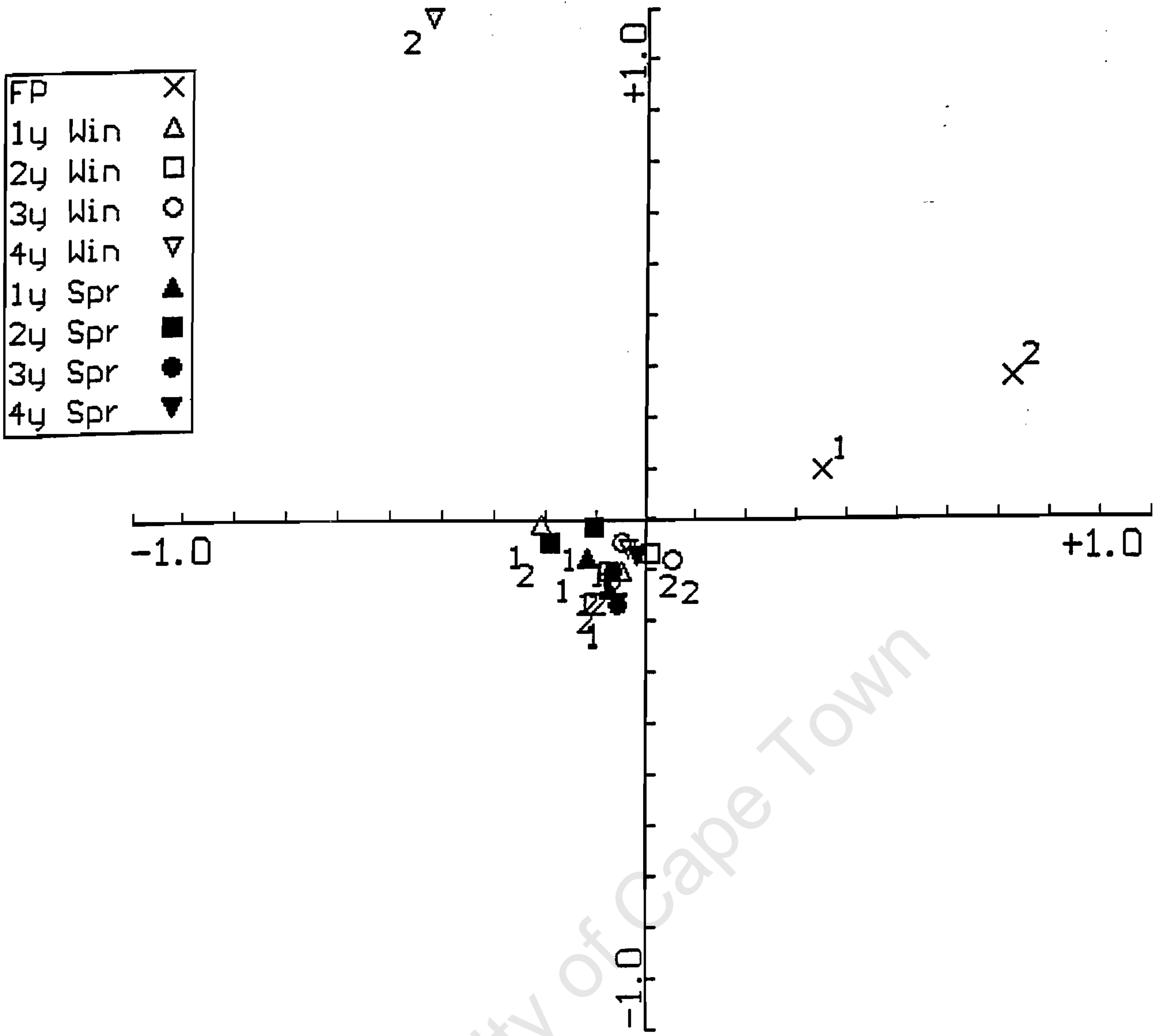


Figure 3.3. Correspondence analysis of the replicates of each treatment sampled in the Honeydale camp 32 trial (numbers represent blocks of replicates).

	Axis 1	Axis 2	Total inertia
Eigenvalues	0.309	0.241	1.912
Cumulative percentage of variance			
- of species data	16.2	28.8	
- of species-environment relations	37.9	55.0	
Sum of all unconstrained eigenvalues			1.912
Sum of all canonical eigenvalues			0.269

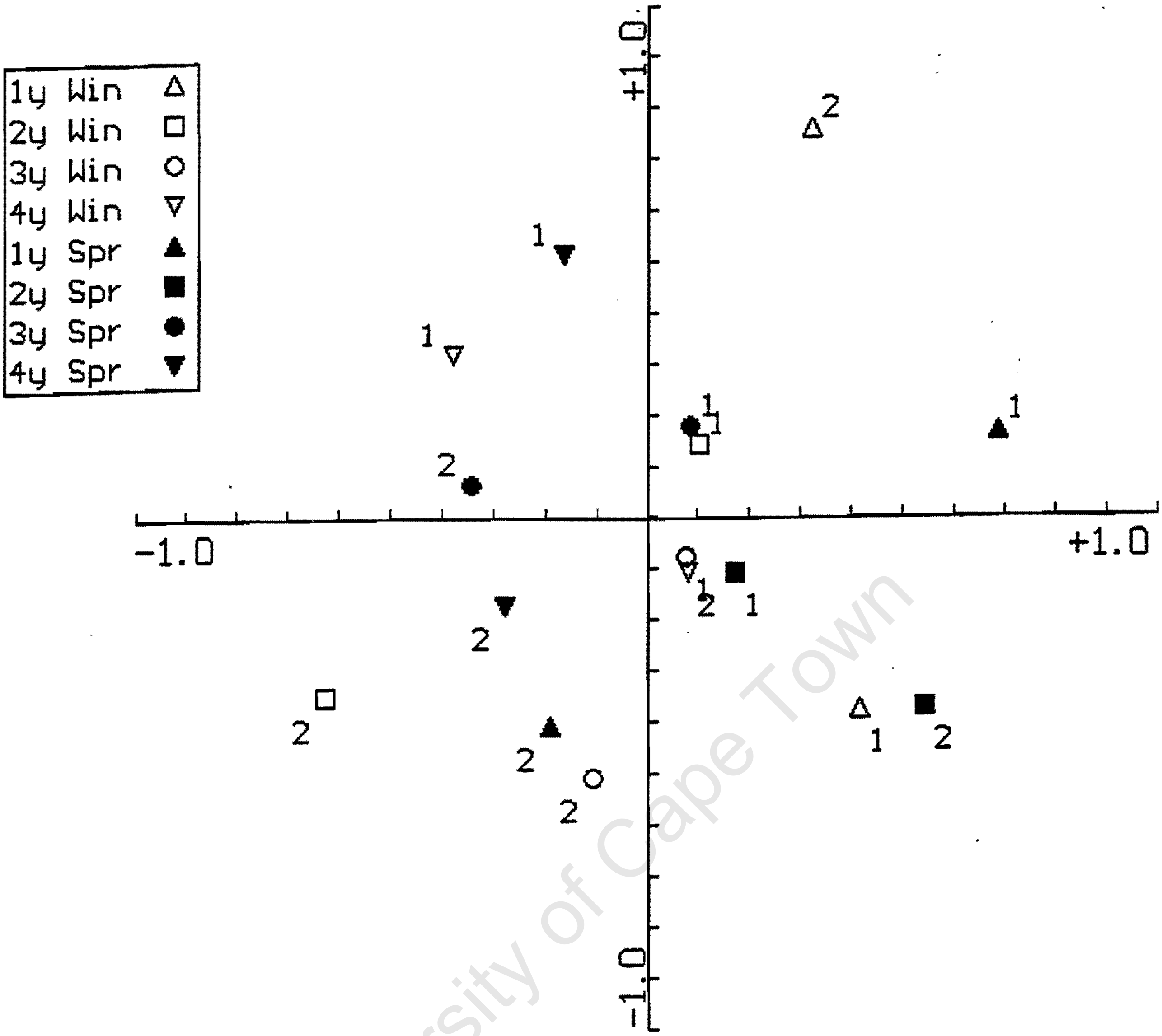


Figure 3.4. Correspondence analysis of the replicates of each burn treatment sampled in the Honeydale camp 32 trial, with the outlier plot passively downweighted (numbers represent blocks of replicates).

	Axis 1	Axis 2	Total inertia
Eigenvalues	0.188	0.183	1.411
Cumulative percentage of variance			
- of species data	13.1	26.2	
- of species-environment relations	33.6	34.3	
Sum of all unconstrained eigenvalues			1.411
Sum of all canonical eigenvalues			0.205

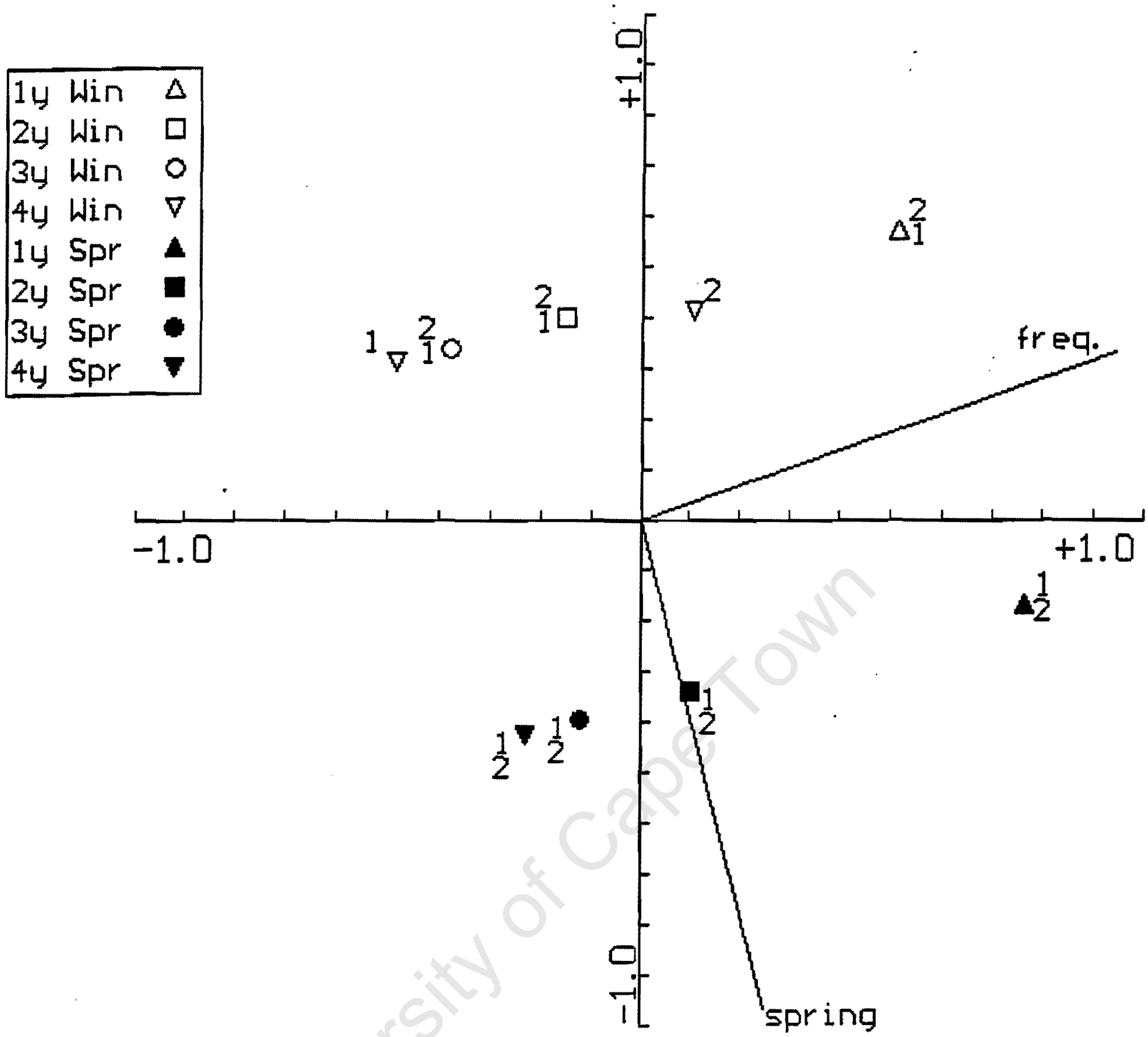


Figure 3.5. Canonical correspondence analysis of the replicates of each burn treatment sampled in the Honeydale camp 32 trial, analysed according to the frequency (freq.) and season of burn, with the outlier plot passively downweighted and a Monte Carlo permutations test performed with 200 permutations (numbers represent blocks of replicates).

	Axis 1	Axis 2	Total inertia
Eigenvalues	0.130	0.075	1.411
Cumulative percentage of variance			
- of species data	9.2	14.5	
- of species-environment relations	63.4	100	
Sum of all unconstrained eigenvalues			1.411
Sum of all canonical eigenvalues			0.205

Monte Carlo permutation test:

	First axis	Overall test
F - ratio	1.22	1.02
P - value	0.31	0.44

INTERMEDIATE DISTURBANCE HYPOTHESIS:

Species richness at 1m^2 showed a slight increase with longer burn intervals. Richness also appeared to be generally higher in the winter than spring burn, though there was little difference in the bi- and triennial burn frequencies (Figure 3.6). Sampled at 100m^2, the mean number of species per treatment increased with decreasing burn frequency (Figure 3.7). Though clear in the spring burn, the increase in species richness in the winter treatment was weakened by the slump at the triennial burn frequency. Thus species richness showed a general increase with decreasing burn frequency at 1m^2 and 100m^2. At both the scales (1m^2 and 100m^2), fire protection produced the highest mean number of species (Figure 3.6 and 3.7).

HETEROGENEITY:

Comparing the slopes and y-intercepts of the regressed species/area relationships, the fire protection and quadrennial burn treatments had the shallowest slopes but the highest y-intercepts (Table 3.3). These were matched by the quadrennial and annual spring burn treatments that had the steepest slopes, but lowest y-intercepts. A single comparison of the slopes between treatments (fire protection versus quadrennial spring burning) had to be excluded due to insufficient homogeneity of slope ($P > 0.05$). However, of the remaining comparisons, only the treatment with the shallowest slope (fire protection) and the two treatments with the steepest slopes (quadrennial and annual spring burns) were significantly different ($P < 0.05$).

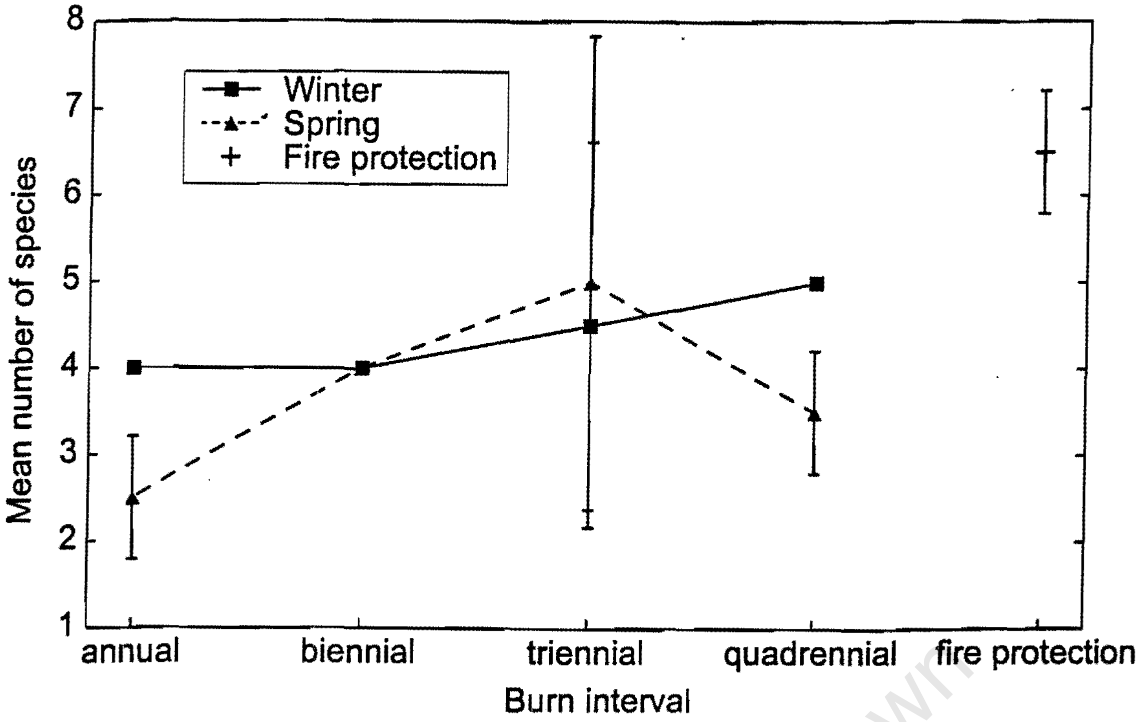


Figure 3.6. Effect of burn frequency on species richness, sampled in different seasons of burn at 1m^2 in the Honeydale camp 32 trial.

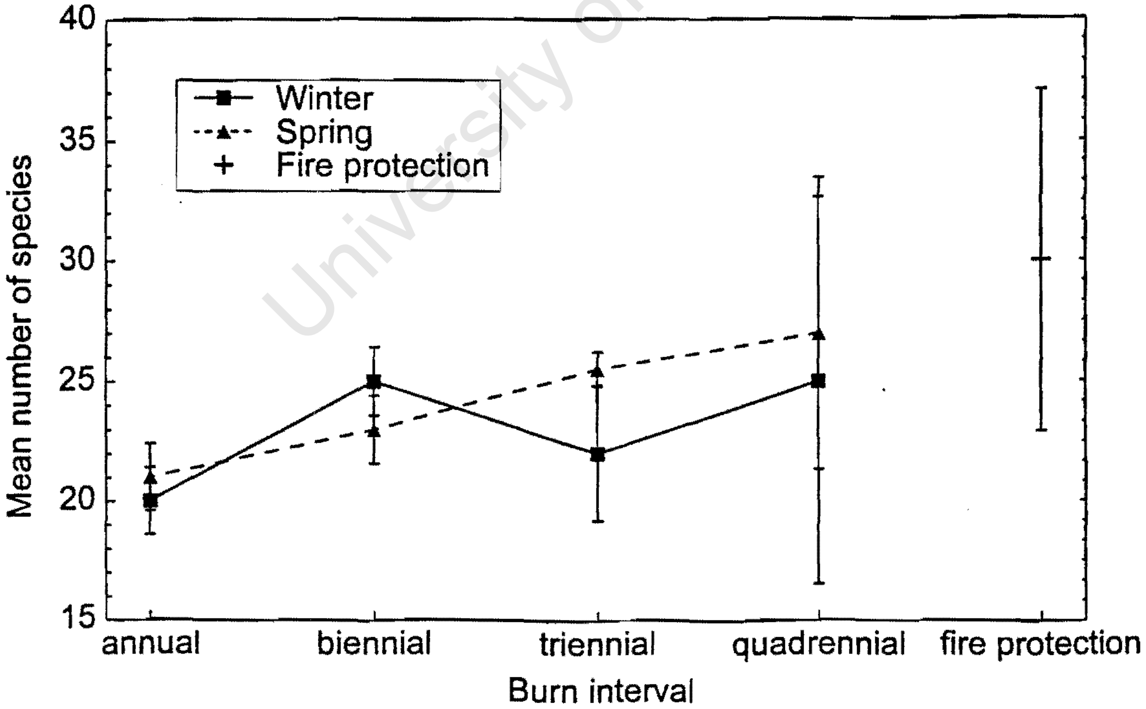


Figure 3.7. Effect of burn frequency on species richness, sampled in different seasons of burn at 100m^2 in the Honeydale camp 32 trial.

Table 3.3. Regression estimates for species/ area curves in the Honeydale camp 32 trial; y = a+bx+eps; y = logarithm of the number of species; x = logarithm of area in m^2; a = Y-intercept; b = slope.

Burn treatments	Y-intercept	Slope	R^2
Annual winter	0.581	0.380	0.957
Biennial winter	0.536	0.409	0.961
Triennial winter	0.575	0.376	0.905
Quadrennial winter	0.691	0.356	0.760
Annual spring	0.413	0.472	0.933
Biennial spring	0.629	0.392	0.905
Triennial spring	0.690	0.385	0.879
Quadrennial spring	0.503	0.479	0.937
Fire protection	0.772	0.354	0.920

DISSIMILARITY COMPARISONS:

The Percentage dissimilarity of species composition within treatments was lowest in the biennial spring burn and highest in the annual spring burn (Table 3.4). Dissimilarity was also low in the triennial spring, biennial winter and fire protection treatments, but showed no clear trends across treatments. Dissimilarity comparisons between treatments were consistently higher between the burn and fire protection treatments than between burn treatments (Figure 3.8). Replicates of the annual and biennial winter, bi- and triennial spring, and fire protection treatments were found to be statistically more similar to each (P <0.05) other than to replicates of other treatments.

HETEROGENEITY ACROSS LARGE PLOTS:

The mean Percentage dissimilarity within the treatments in the camp 22 trial, was highest in the biennial and quadrennial burns (Table 3.5). The dissimilarity between the replicates of these two treatments was also the most different, as

Table 3.4 Mean Percentage dissimilarity in the species composition between replicates (sampled at $100m^2$) of each treatment in the Honeydale camp 32 trial.

Burn treatments	Percentage dissimilarity
Annual winter	48.71
Biennial winter	46.02
Triennial winter	50.68
Quadrennial winter	52.37
Annual spring	64.17
Biennial spring	41.03
Triennial spring	45.40
Quadrennial spring	51.15
Fire protection	46.23

	1y Win	2y Win	3y Win	4y Win	1y Spr	2y Spr	3y Spr	4y Spr	FP
1y Win									
2y Win	52.09								
3y Win	50.52	48.79							
4y Win	48.79	52.19	54.88						
1y Spr	51.95	53.42	49.79	56.46					
2y Spr	45.51	48.95	49.27	46.74	50.81				
3y Spr	47.54	45.76	47.49	48.39	51.69	46.85			
4y Spr	50.83	45.66	50.79	49.45	53.23	52.89	50.79		
FP	59.37	52.42	52.19	58.23	59.99	58.32	52.31	52.35	

Figure 3.8. Percentage dissimilarity in the species composition between treatments of the Honeydale camp 32 trial; calculated as the mean dissimilarity between the replicates (sampled at $100m^2$) of the treatments being compared.

indicated by the high standard deviation scores. The fire protection and annual burn treatments were the most homogeneous and the replicates corresponded. The mean Percentage dissimilarity was, however, not statistically different (*P* >0.05) between any of the treatments. Thus, no clear trends in the long term effects of burn frequency on vegetation patchiness were noted.

Table 3.5. Mean Percentage dissimilarity in the treatments of the Honeydale camp 22 trial, sampled as the dissimilarity in the species composition between 25 x $2m^2$ quadrats in both replicates of each treatment (*P* >0.05 between all treatments).

Burn treatment	Mean Percentage dissimilarity	Standard deviation
Annual burn	51.32	2.70
Biennial burn	59.53	10.04
Triennial burn	55.33	1.05
Quadrennial burn	58.08	12.88
Sexennial burn	54.34	6.36
Fire protection	50.17	2.72

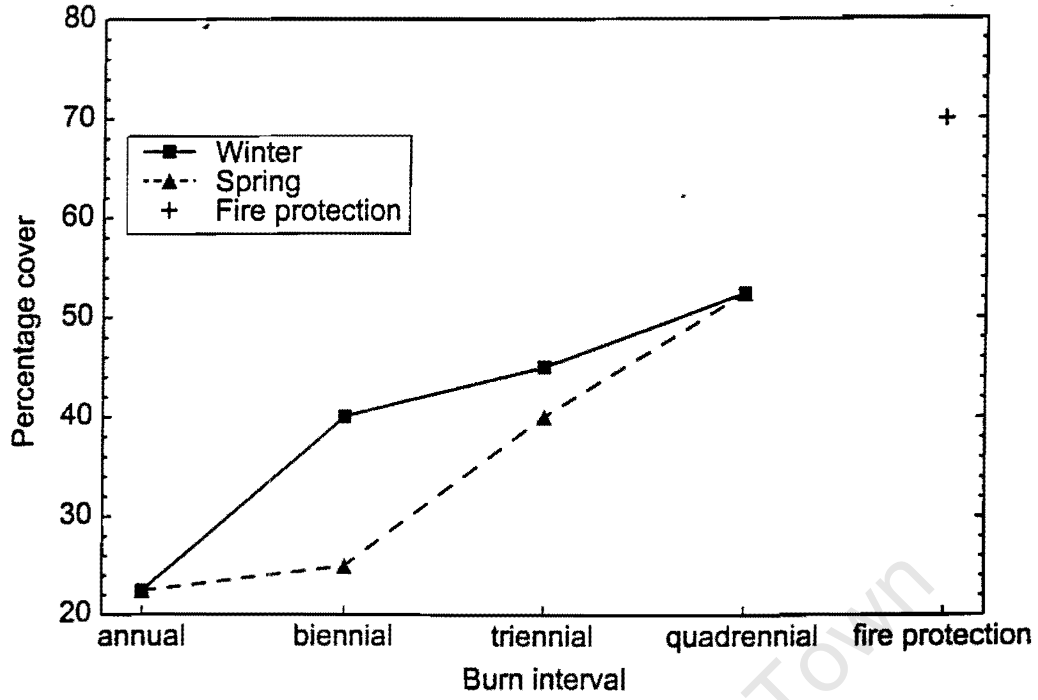
SWARD ATTRIBUTES:

PERCENTAGE COVER:

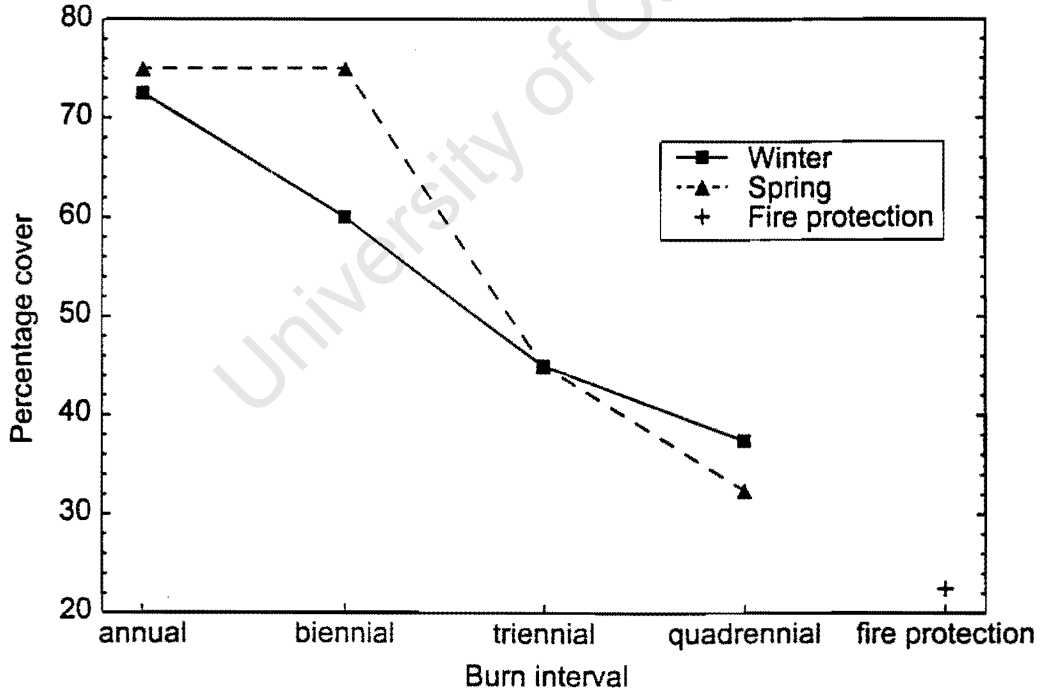
Aerial cover at Honeydale was completely dominated by two grasses, *Cymbopogon plurinodis* and *Themeda triandra* (Table 3.6). All but one of the remaining species constituting the aerial cover were grasses, *Berkheya heterophylla* being the only forb. *Berkheya* cover, however, showed no discernable pattern of distribution across either frequency or season of burn. The grass, *Heteropogon contortus*, was present in a single plot, the

Table 3.6. Percentage cover estimates, averaged from the two replicates of each treatment in the Honeydale camp 32 trial.

		1y Win	2y Win	3y Win	4y Win	1y Spr	2y Spr	3y Spr	4y Spr	FP
Forb	*Berkheya spp.*	0	0	10	0	2.5	0	15	7.5	0
Grasses	*Cymbopogon plurinodis*	22.5	40	45	52.5	22.5	25	40	52.5	70
	Eragrostis capensis	2.5	0	0	0	0	0	0	0	0
	Eragrostis curvula	2.5	0	0	0	0	0	0	2.5	0
	Eustachys paspaloides	0	0	0	2.5	0	0	0	0	0
	Helictotrichon turgidulum	0	0	0	2.5	0	0	0	2.5	0
	Heteropogon contortus	0	0	0	5	0	0	0	0	0
	Melica decumbens	0	0	0	0	0	0	0	0	7.5
	Panicum maximum	0	0	0	0	0	0	0	2.5	0
	Themeda triandra	72.5	60	45	37.5	75	75	45	32.5	22.5



Cymbopogon plurinodis



Themeda triandra

Figure 3.9. Effect of frequency and season of burn, after 25 years of continuous treatment, on the species that dominated the aerial cover of the Honeydale camp 32 trial.

quadrennial winter burn in the second block of replicates, that had appeared as an outlier in the ordination (Figure 3.3). The remaining grass species occurred throughout the trial, but seldom constituted large enough percentages of the aerial cover to merit inclusion (Table 3.6). Graphed against burn frequency for the winter and spring burns, the aerial cover represented by *C. plurinodis* increased with decreasing frequency of burn (Figure 3.9). The aerial cover constituted by *T. triandra* showed the inverse of this, decreasing with burn frequency (Figure 3.9).

LIGHT ATTENUATION:

Light attenuation curves for the annual and quadrennial spring burns indicated that the sward in the quadrennial burn treatment was marginally taller (Figure 3.10). Whereas the sward in the annual burn only started to increase its F below 300mm off the ground, the sward in the quadrennial burn reached over 400mm at the time of sampling. The difference between F for the two treatments was greatest in the middle of the sward, converging towards the bottom of the sward. The differences between F values were, however, very small compared to those for Ukulinga (Figure 2.11). According to the standard deviation around F for the two treatments, they did not differ significantly down through the sward.

BIOMASS:

Though biomass was the same in the annual burns, as burn interval increased, biomass in the winter burn plots peaked in the bi- and triennial burn treatments while the spring burn treatments slumped. Thereafter, however, the quadrennial spring burn recorded the highest biomass while the biomass in the winter burn decreased (Figure 3.11).

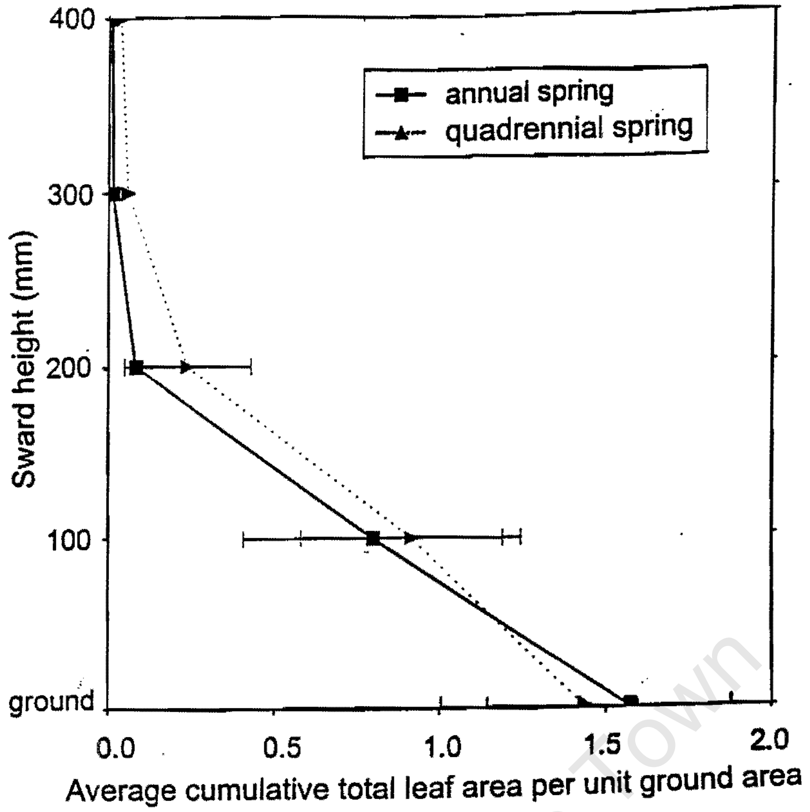


Figure 3.10. Effect of burn frequency on light attenuation down the sward in the Honeydale camp 32 trial, averaged from ten sets of readings in each replicate of the shortest and longest spring burn treatments.

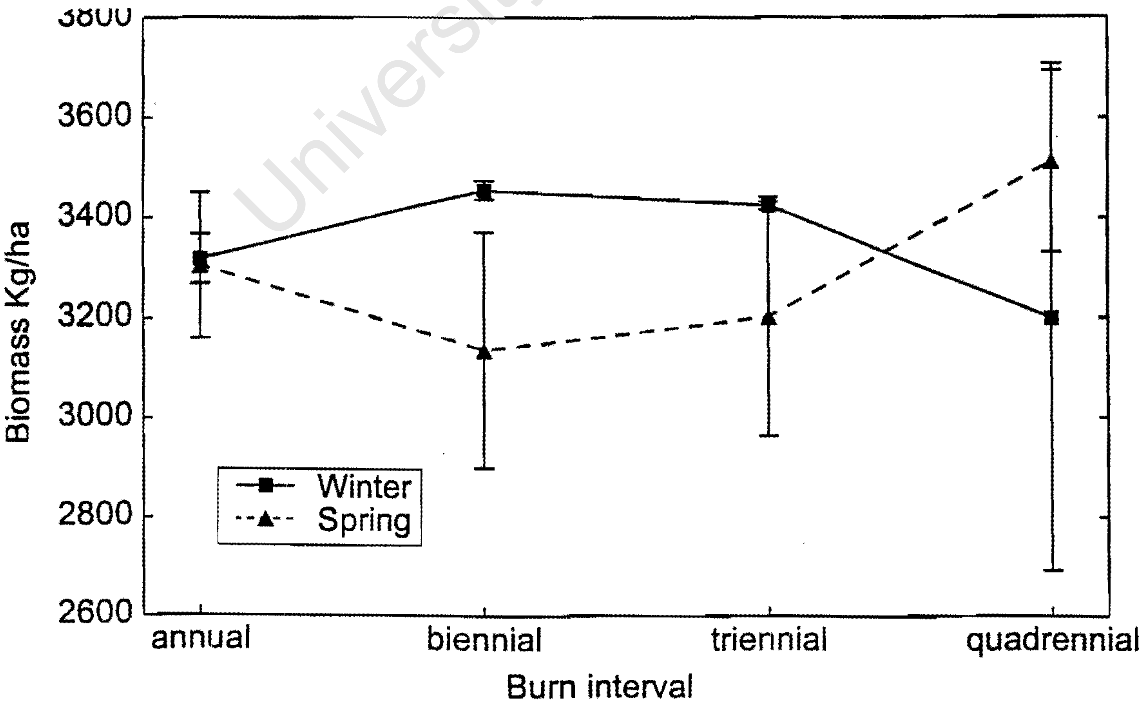


Figure 3.11. Influence of frequency and season of burn on sward biomass in the Honeydale camp 32 trial.

3.5 DISCUSSION

THE EFFECT OF FREQUENCY AND SEASON OF BURN:

Alpha diversity sampled at $1m^2$ and $100m^2$ showed a weak increase in species richness with decreasing fire frequency (Table 3.1). Though there was no support for the IDH (Figures 3.6 and 3.7), this result matched findings from the North American tall grass prairies (Collins & Gibson 1990; Collins, Glen & Gibson 1995). Biomass also appeared to respond to the season of burn, with winter burns having a higher production than the spring burns at intermediate burn frequencies (Figure 3.11). Burning treatments coincided in 1997, with only annual burn being repeated once prior to sampling. Thus, the lower biomass in the quadrennial winter and bi- and triennial spring treatments than both annual burns is difficult to explain as the annual burns had a season's less growth than them. Sampling, however, was done early in the season well before the sward had reached its peak biomass. With little difference in the post-burn age between the annual and quadrennial spring treatments, burn frequency was not seen to have a significant impact on the sward structure (Figure 3.10). The significantly lower F values down the sward at Honeydale than Ukulinga may be ascribed to sampling having been done early in the growing season, before the sward had reached its peak.

BURNING VERSUS FIRE PROTECTION:

The differences noted in the species composition between the burn and fire protection treatments at Ukulinga were even more pronounced at Honeydale (Figure 3.3). This was also obvious in the high proportion of rare species in the fire protection treatment, compared to the burn treatments (Table 3.2). Comparisons of the dissimilarity in species composition between treatments further suggested that the burn treatments were more similar to each other than to the fire protection treatment (Figure 3.8). Though the burn treatments had all recently been burnt, the fire protection treatment had not been burnt for over 25 years. This implied a directional succession of species under fire protection.

RESPONSES TO BURNING:

The most striking pattern noted at Honeydale was the domination of the aerial cover by two grass species, *Cymbopogon plurinodis* and *Themeda triandra*, and their clear and opposite response to fire frequency and season (Figure 3.9). These results support the findings of a previous study conducted in the plots, at least for the frequency of burn as seasonal effects were not previously tested (Robinson *et al.* 1979). Implicit in this observation, was the apparent lack of clear response to fire frequency and season by the majority of species. With limited post-burn successional differences between the burn treatments, ordination showed that environmental gradients across the site were having more of an impact on species composition than the frequency and season of burn (Figure 3.4). This conclusion also supported the findings of Robinson *et al.* (1979) and was backed up by the low number of rare species in the burn treatments, and high proportion of these that were shared between burn treatments (Table 3.2).

SPECIES COMPOSITION:

Due to each treatment only being represented by two replicates, the distribution of species and rare species across the replicates of each burn treatments was not a good indicator of how strongly treatments were influencing species composition (Tables 3.1 and 3.2). This also meant that the proportion of the total number of species per treatment found in each replicate was expected to be higher than the other sites (Table 3.1). Even so, this measure still gave no indication that the frequency and season of burn were influencing the similarity of the species composition of the treatments' replicates. This conclusion was further supported by the absence of clear trends between the within treatment dissimilarity measures in both the small and large scale plots (Tables 3.4 and 3.5). The absence of clear patterns in vegetation patchiness, as described by the slope of the species/area curve, may therefore be explained by species not having been favoured by particular burning treatments (Table 3.3).

SUMMARY:

Thus, alpha diversity at 1m^2 and 100m^2 showed weak trends across fire frequency in the range of 1 - 4 years and fire season in winter and spring, but provided no support for the IDH. Species composition of the burn treatments was shown to differ from that under fire protection, implying a directional succession of species with fire protection. Species composition of the burn treatments responded more to environmental gradients than to frequency and season of burn treatments. Therefore, as the burn treatments were all at a similar successional stage, species turnover between treatments was a result of species/area relations. The most striking pattern though was clear and opposite responses to frequency and season of burn shown by the two dominant grasses.

KWAZULU-NATAL DRAKENSBERG

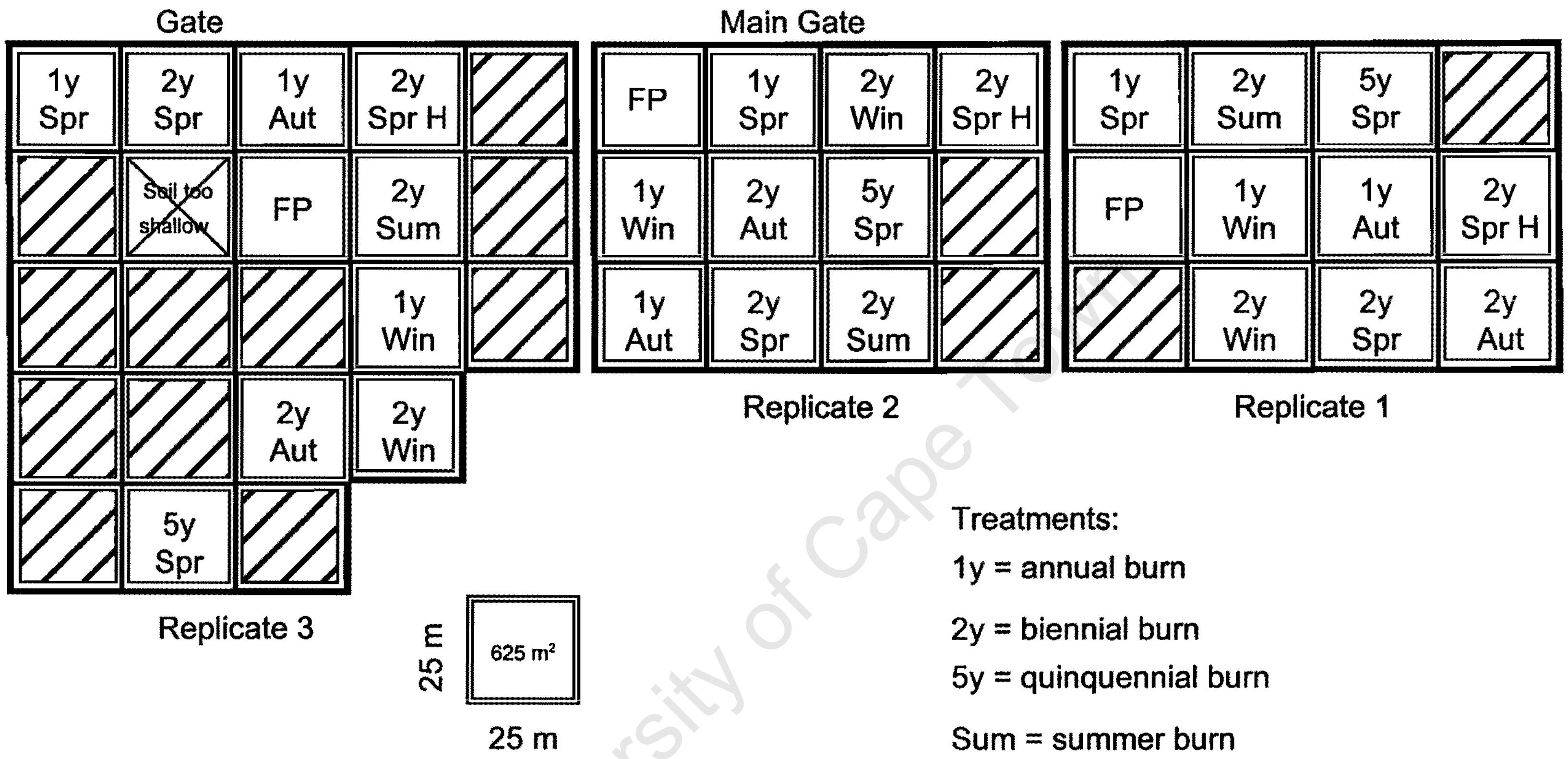
4.1 INTRODUCTION

The montane region of the eastern escarpment, that forms the KwaZulu-Natal Drakensberg, represents an area of high rainfall. In frequently burnt swards, dense, middle grass swards dominated by *Themeda triandra* occur, with succession to scrub and forest taking place under fire protection (Tainton & Mentis 1984). Due to their significance as South Africa's principal catchment area, the Drakensberg mountains have attracted a large amount of research and management efforts. The region is also considered to be one of the floral "hot spots" of endemism in southern Africa and therefore has great conservation importance (Cowling & Hilton-Taylor 1994; Scott-Shaw 1999). Botanical exploration in the region has been dealt with in detail by Killick (1990) in his chapter titled "Plant Exploration". In 1938 the Department of Forestry decided to investigate the effects of afforestation on water supplies on the lower slopes of the Drakensberg in KwaZulu-Natal. A series of long term studies on the hydrology, meteorology and plant ecology were initiated in the Cathedral Peak research area for this purpose. Later, the trials examined in my study (which are currently the only long-term defoliation trials running in the Drakensberg) were initiated to examine various aspects of, among other things, veld burning (Stuckenberg, Meester & Bainbridge 1978). Research findings from these trials and work done at Giant's Castle Game Reserve (Scotcher, Rowe-Rowe, Clarke & Lowry 1980) and Royal Natal National Park (Burgess 1991) have provided the basis of burning practices for the whole region which have often been extended to the KwaZulu-Natal Midlands (see for example Everson & Tainton 1984; Tainton & Mentis 1984). In my study, the trials were used to examine the effects of frequency and season of burn on various aspects of phytodiversity, using a variety of methods. The predictions of the IDH were then tested according to these diversity measures. The trials were also used to examine the effects of frequency and season of burn on vegetation patchiness at point and landscape scales; and on sward composition, structure and biomass.

4.2 SITE DESCRIPTION

Two trials in the Cathedral Peak section of the Mlambonja Wilderness Area in the KwaZulu-Natal Drakensberg, South Africa (29°00'S 29°15'E) were sampled (Figure 1.1). The Brotherton trial and Cathedral Peak research catchments are maintained by the KwaZulu-Natal Nature Conservation Service (KZNNCS). Located in the mountainous terrain of the Moist Upland Grasslands (Bredenkamp, Granger, Lubke & van Rooyen 1996: Vegetation type 42), with 1380mm mean annual precipitation, the vegetation is dominated by the grass, *Themeda triandra*. Sampling of both trials was done in January and February of 1999.

The Brotherton trial (Figure 4.1) is situated on the Brotherton spur 1890m above sea level. Established in 1980, the trial was initiated to examine the long-term effects of different seasons and frequencies of defoliation on the fire-climax grasslands of the KwaZulu-Natal Drakensberg (Morris, Dicks, Everson & Everson 1999). The trial consists of fire, mowing and chemical defoliation treatments arranged in a random block design. Of the 21 treatments, twelve are replicated in three plots (25 x 25m); with the remaining nine treatments serving as nonreplicated demonstration plots. For the purposes of my study only the replicated burning treatments were sampled. These included a biennial summer burn; annual and biennial autumn burns; annual and biennial winter burns; annual, biennial low intensity "cool" (head burn), biennial high intensity "hot" (back burn) and quinquennial spring burns;



▨ Hatched plots were not sampled as their treatments were either not replicated or inappropriate to the aims of this study.

Treatments:

1y = annual burn

2y = biennial burn

5y = quinquennial burn

Sum = summer burn

Aut = autumn burn

Win = winter burn

Spr = spring burn

Spr H = spring hot burn

FP = fire protection

Figure 4.1. Layout of plots sampled in the Cathedral Peak Brotherton trial.

and a fire protection treatment which had not been burnt since the trial commenced in 1980. Excluding the quinquennial spring burns, all the burn treatments sampled in this trial coincided in the year prior to sampling. Of the three replicates of the quinquennial spring burn, one had accidentally been burnt the year before sampling. The other two replicates of this treatment were due to be burnt later in the same year as the sampling was done, and were thus close to completing their full five years of fire protection.

The 15 research catchments (numbered I to XV) (Figure 4.2) are located in the research area at Cathedral Peak. They vary in size from 265000m^2 to 947000m^2, and range in elevation from 1800m to 2600m above sea level. The catchments represent a range of treatments, initiated to examine the influence of fire frequency and season, and afforestation on the vegetation and water yield in mountain catchments. The treatments sampled included the biennial summer burn (February/March) in catchment VIII; the biennial autumn burn (May/June) in catchment VI; the biennial winter burn (June/July) in catchment I; the biennial spring burn (August/September) in catchment X; the octennial spring burn rotation (August/September) in catchment XIII; and two fire exclusion treatments in catchments IX and XV initiated in 1952. The remaining catchments had either been afforested with *Pinus patula* or were replicates that did not coincide on the burning timetable and were therefore not sampled. All catchments were surrounded by a fire-break burnt in June/July as part of the winter burns.

4.3 MATERIALS AND METHODS

4.3.1 Data collection

IMPORTANCE-SCORE METHOD:

The Brotherton trial was sampled using the importance-score method (Chapter 2.3.1). Quadrats were erected by calculating the position of the first pole from the corner of the plot, to centre the quadrat in the plot as done for Ukulinga. This position was calculated as half the difference between the width of the plot (25m) and the width of the largest sub-quadrat (10m) (Chapter 2.3.1).

BETA DIVERSITY:

The research catchments at Cathedral Peak were sampled using belt transects (Figure 4.2). Ten paired samples were taken in the catchment and adjacent fire-break. Paired quadrats (25m x 4m) were spaced along one side of the catchment to equally represent the steep upper, flat middle and steep lower slopes. Care was taken to located quadrat pairs on similar types of terrain. Each sample was made by laying down a 25m string approximately ten meters in from, and parallel to, the catchment/fire-break boundary. All the species occurring two meters on either side of this string were then recorded.

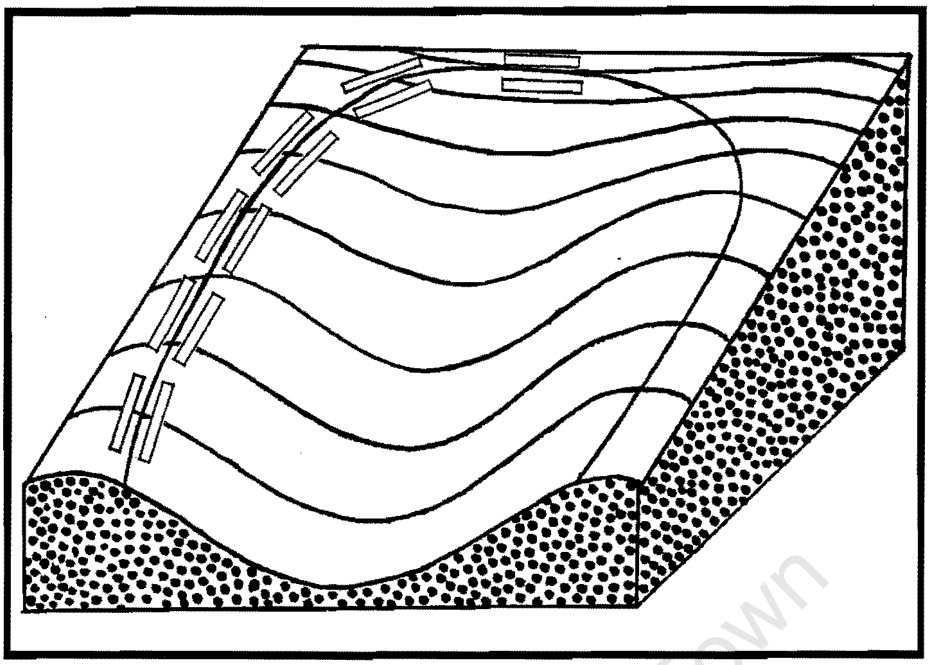


Figure 4.2. Diagrammatic representation of the top half of a catchment showing the layout of pairs of quadrats in the catchment and its adjoining fire-break.

SWARD ATTRIBUTES:

PERCENTAGE COVER:

Percentage cover estimates were made in each of the Brotherton burning plots as done at Ukulinga (Chapter 2.3.1).

LIGHT ATTENUATION:

Ten sets of light attenuation readings were taken in each of the annual and quinquennial spring burn replicates in the Brotherton trial, as done at Ukulinga (Chapter 2.3.1).

BIOMASS:

The mass of standing green material in the Brotherton burning plots was measured using a disc pasture meter as done at Honeydale (Chapter 3.3.1).

4.3.2 Data analysis

Except for ordination, the data collected from the Brotherton trial by the importance-score method; the percentage cover estimates; and the light attenuation data was all analysed in the same fashion as the data from Ukulinga (Chapter 2.3.2).

ORDINATION:

The first ordination performed on the data collected by the importance-score method was analysed using a CA with a passive analysis of environmental variables. In the second CA with a passive analysis of environmental variables, the fire protection plots were removed from the ordination to explore the effect of the burning treatments. The quinquennial spring burn treatments were also passively down weighted in this analysis to reduce any differences that may have resulted from their replicates being of different age since last burn. Lastly, a CCA with the same modifications as the last CA was performed, with a Monte Carlo Test with 200 random permutations.

BETA DIVERSITY:

The effect of various fire treatments on vegetation patchiness, at the landscape level, was tested in the Cathedral Peak catchments. As the catchments differed in a range of environmental factors, such as aspect of slope, elevation and area covered, means were sought to standardise comparisons between them. This was achieved by comparing the species composition in each catchment to that of the fire-breaks that surrounded the catchments. As all the fire-breaks were burnt annually at the same time, they provided a uniform treatment abutting each catchment against which the catchment could be standardised to exclude the environmental differences between catchments. Percentage dissimilarity in species composition was calculated across the ten transects sampled in the catchments (treatment) and their fire-breaks (control) using Releve Manager 1.08. Comparisons between catchments were then standardise by subtracting the beta diversity of the control from that of the fire treatment.

As the standardised beta diversity did not provide clear trends across the fire treatments, it was necessary to examine whether treatments were determining species composition. To do this, the mean dissimilarity between fire treatment and control transect pairs was calculated for each catchment. This mean dissimilarity was then compared at the 95 percent confidence interval using the STATISTICA 5.1 Tukey, HSD MANOVA. Based on the alpha diversity results, it was predicted that the biennial burn treatments should be more similar to their annually burnt controls than the octennial and fire protection treatments were.

These results were further explored by calculating the proportion of species common or unique to the catchment (C) and fire-break (*FB*) in a transect pair (*TP*). This was computed as the mean ($\bar{x}$) and standard deviation (s_x) of the number of species, expressed as a percentage of the total number of species in the transect pair. As defined by the formulas:

$$\bar{x} = \frac{1}{n}\sum_{i=1}^{n}\left(\frac{x_i}{TP}\times\frac{100}{1}\right)$$

$$S_x = \sqrt{\Sigma\left(\frac{x_i}{TP}\times\frac{100}{1}\right)^2 - \frac{1}{n}\left(\Sigma\frac{x_i}{TP}\times\frac{100}{1}\right)^2 \Big/ (n-1)}$$

where: x = the number of species either common to both *C* and *FB* in a *TP*, or unique to *C* or *FB*

n = number of replicates

SWARD ATTRIBUTES:

BIOMASS:

Biomass of the burn treatments from the Brotherton trial was calculated from the disc pasture meter readings using the calibration equation developed by Everson (1985) for the Cathedral Peak area:

$y = 24.45x - 49.27$

where: y = estimated standing grass crop ($g.m^{-2}$)

x = mean disc height (cm)

The biomass data calculated in this way was converted to $Kg.ha^{-1}$ and analysed in the same manner as described for Ukulinga (Chapter 2.3.2).

4.4 RESULTS

SPECIES RICHNESS:

In the treatments sampled from the Brotherton trial, species richness showed no clear trends according to either the frequency or season of burn (Table 4.1). On average, each treatment contained nearly 55 percent of the 89 species recorded in the trial. Treatments with high percentages of their species occurring in all three replicates (annual winter, biennial summer, biennial autumn and biennial winter) also had high mean numbers of species per replicate, expressed as a percentage of the total number of species in the treatment. In the quintenial spring burn and fire protection treatments over half of the species only occurred in one replicate of the treatment. Each replicate also constituted the lowest proportions of the total number of species in these two treatments. However, the mean number of species per replicate, expressed as a percentage of the total number of species in the treatment did not differ significantly between any treatments ($P > 0.05$).

Table 4.1. Species richness of the various treatments sampled from the Cathedral Peak Brotherton trial. Species were sampled from a 100m^2 quadrat in each of the three replicates per treatment; x = number of species in a replicate; y = total number of species in a treatment; z = total number of species at the site (89); n = number of replicates per treatment (3); $\bar{x}$ = mean percentage; S_x = percentage standard deviation.

	2y Sum	1y Aut	2y Aut	1y Win	2y Win	1y Spr	2y Spr	2y Spr H	5y Spr	FP
y	49	48	45	47	52	49	47	47	55	48
$\frac{y}{z} \times \frac{100}{1}$	55	53.9	50.6	52.8	58.4	55	52.8	52.8	61.8	53.9
Percentage of species in each treatment:										
occurring in one replicate.	29	42	27	36	27	47	40	34	55	52
occurring in two replicates.	24	25	29	17	35	22	28	36	20	21
occurring in all three replicates.	47	33	44	47	38	31	32	30	25	27
$\bar{x} = \frac{1}{n}\sum_{i=1}^{n}\left(\frac{x_i}{y} \times \frac{100}{1}\right)$	72.8	63.9	74.8	70.2	70.5	61.9	65.3	67.4	57	58.3
$S_x = \sqrt{\Sigma\left(\frac{x_i}{y} \times \frac{100}{1}\right)^2 - \frac{1}{n}\left(\Sigma \frac{x_i}{y} \times \frac{100}{1}\right)^2 \Big/ (n-1)}$	4.2	16.8	1.3	2.1	9.5	1.2	2.5	6.5	15.9	7.2

(P >0.05 between all treatments).

Table 4.2. Treatment effects on rare species (species occurring in ≤ three plots) in the Cathedral Peak Brotherton trial. The number of rare species recorded for the annual autumn treatment was significantly lower, and the number of rare species recorded for the fire protection treatment significantly higher (at the 95 percent confidence interval) than what was expected according to the linear regression of the number of rare species against the total number of species recorded for each treatment.

	2y Sum	1y Aut	2y Aut	1y Win	2y Win	1y Spr	2y Spr	2y Spr H	5y Spr	FP
Total number of species.	49	48	45	47	52	49	47	47	55	48
Number of rare species.	4	2	2	4	5	4	4	4	9	10
Percentage of the species that are rare.	8.2	4.2	4.4	8.5	9.6	8.2	8.5	8.5	16.3	20.8
Number of rare species:										
only occurring in this treatment.	1	1	1	2	2	2	2	1	4	7
occurring in this and one other treatment.	1	1	1	2	2	0	0	3	4	2
occurring in this and two other treatments.	2	0	0	0	1	2	2	0	1	1
Number of rare species for each treatment:										
only occurring in one replicate.	4	2	2	4	5	4	4	4	9	9
occurring in two replicates.	0	0	0	0	0	0	0	0	0	0
occurring in all three replicates.	0	0	0	0	0	0	0	0	0	1

Of the 89 species recorded in the Brotherton trial, 34 (38 percent) were considered rare for the trial as they occurred in three or less of the plots sampled (Table 4.2). The burning treatments showed little variation in the numbers of rare species each possessed. The fire protection and quinquennial burn treatments, however, contained double the number of rare species found in the burn treatments. The fire protection treatment had the highest number of rare species that were unique to this treatment, whereas the rest of the treatments shared at least half of their rare species with other treatments. Except for a single rare species that occurred in all three replicates of the fire protection treatment, all the rare species occurred in only one replicate of the treatments they were found in.

ORDINATION:

Barring one replicate of the quinquennial spring burn, treatments in the first CA separated out on the first axis into burn and fire protection treatments (Figure 4.3). Plots were grouped on the second axis according to the block of replicates in which they occurred. This implied the presence of an underlying environmental gradient in the trial (Figure 4.3). When the burn treatments were considered separately with the quinquennial spring burn passively down weighted, the plots separate out on the first axis relative to their position at the site (Figure 4.4). In particular, replicates from the third block separated out from the other two blocks along the first axis (Figure 4.4). This confirmed the role that environmental gradients occurring at the site were having on species composition.

Constrained in a CCA according to the frequency and season of burn, burn treatments only accounted for 22.3 percent of the total variance (Figure 4.5). Of this, only 48 percent of the species-environment relations were explained

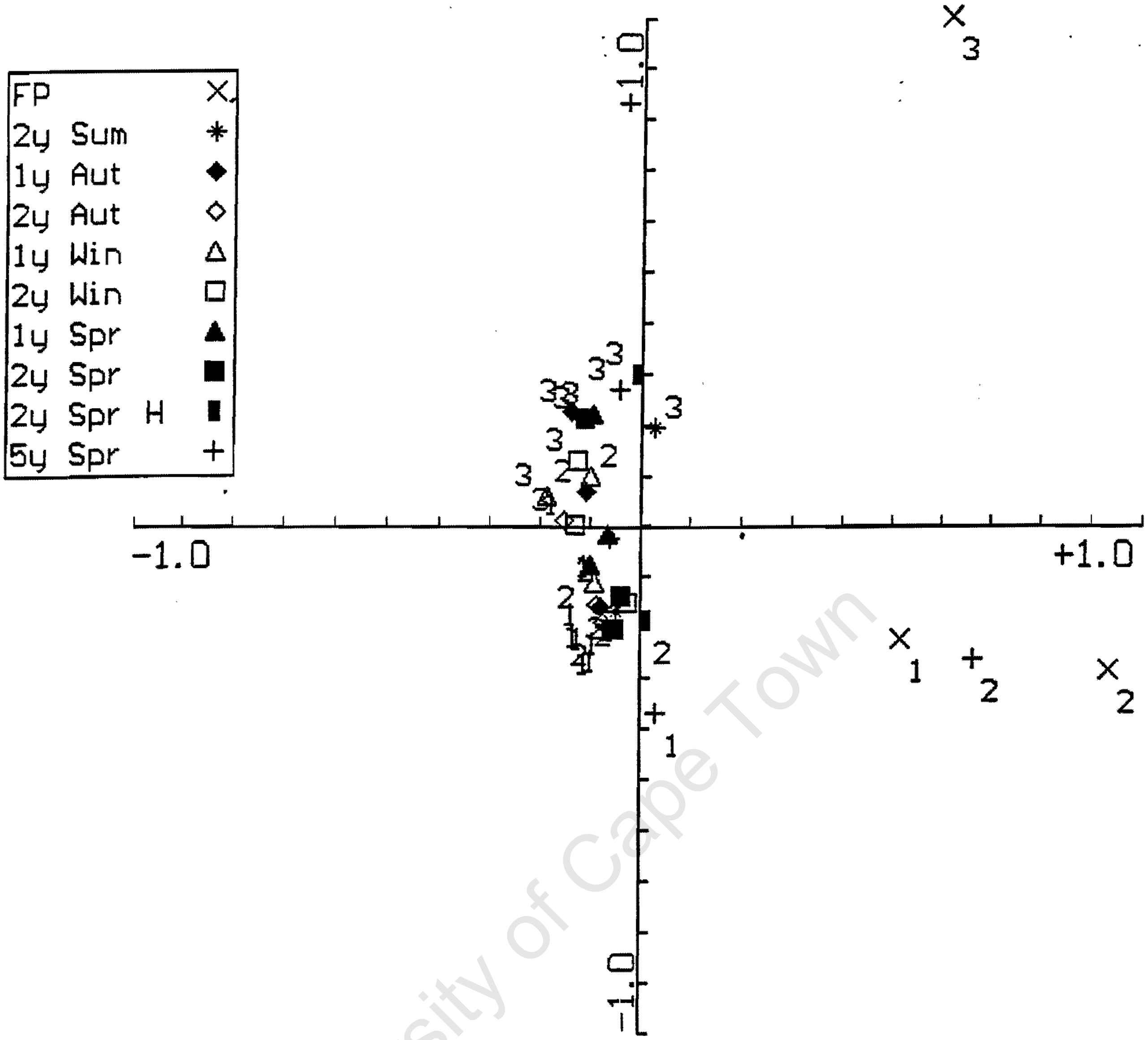


Figure 4.3. Correspondence analysis of the replicates of each treatment sampled in the Cathedral Peak Brotherton trial (numbers represent blocks of replicates).

	Axis 1	Axis 2	Total inertia
Eigenvalues	0.222	0.126	1.550
Cumulative percentage of variance			
- of species data	14.3	22.5	
- of species-environment relations	40.6	42.7	
Sum of all unconstrained eigenvalues			1.550
Sum of all canonical eigenvalues			0.412

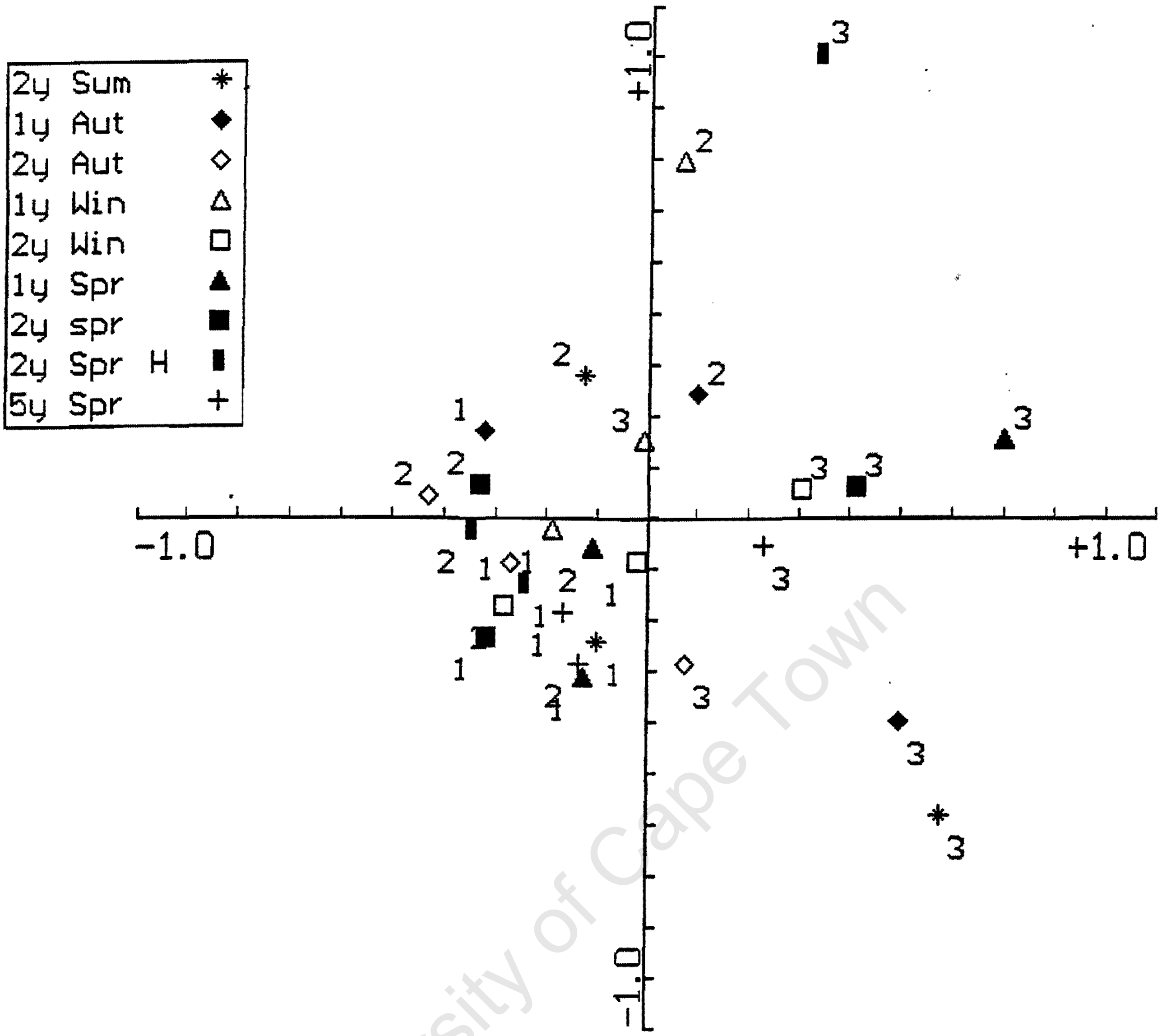


Figure 4.4. Correspondence analysis of the replicates of each burn treatment sampled in the Cathedral Peak Brotherton trial (numbers represent blocks of replicates).

	Axis 1	Axis 2	Total inertia
Eigenvalues	0.121	0.100	1.117
Cumulative percentage of variance			
- of species data	10.8	19.7	
- of species-environment relations	4.8	12.6	
Sum of all unconstrained eigenvalues			1.117
Sum of all canonical eigenvalues			0.249

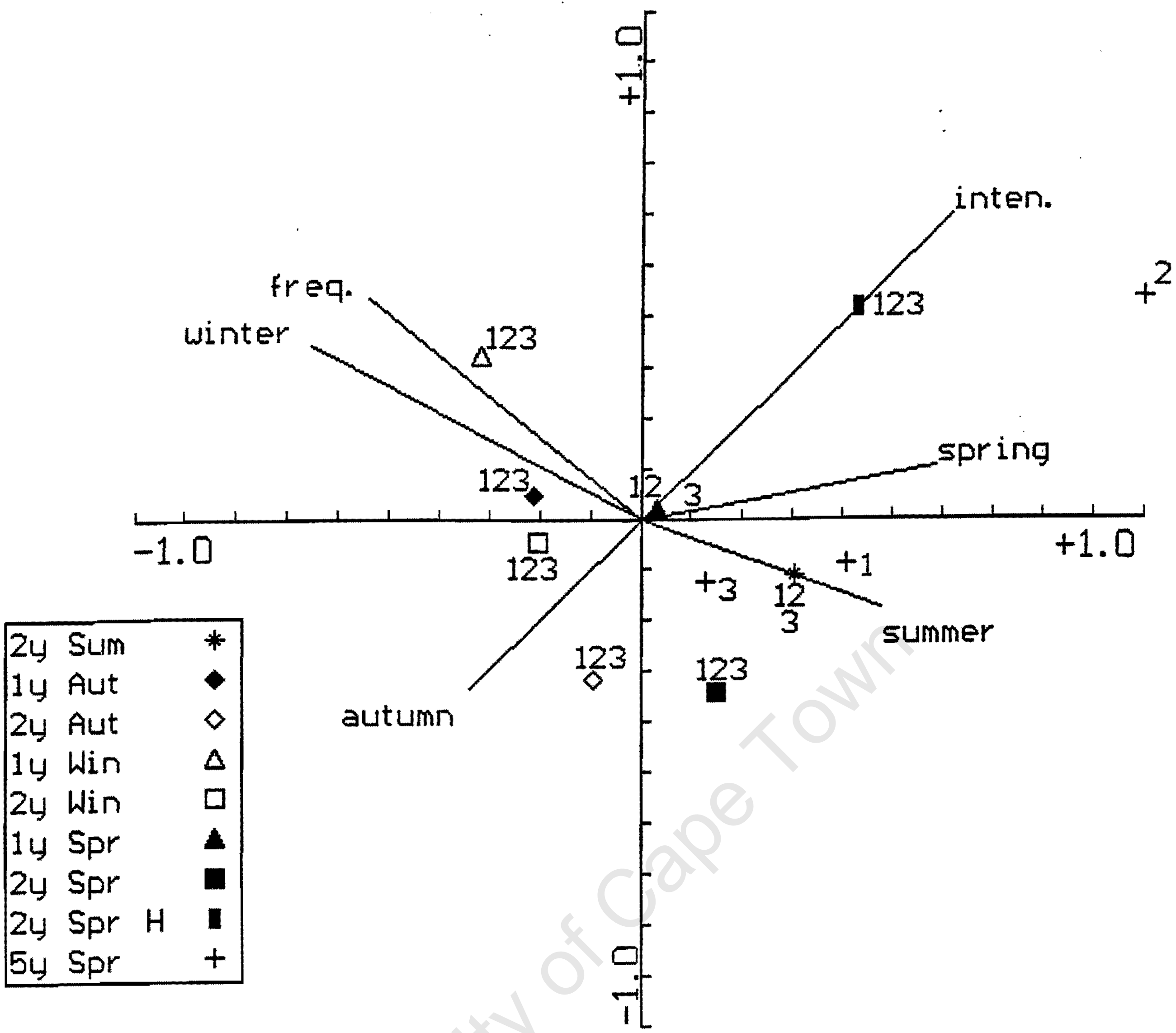


Figure 4.5. Canonical correspondence analysis of the replicates of each burn treatment sampled in the Cathedral Peak Brotherton trial, analysed according to the frequency (freq.), season and intensity (inten.) of burn with a Monte Carlo permutations test performed with 200 permutations (numbers represent blocks of replicates).

	Axis 1	Axis 2	Total inertia
Eigenvalues	0.066	0.054	1.117
Cumulative percentage of variance			
- of species data	5.9	10.7	
- of species-environment relations	26.5	48	
Sum of all unconstrained eigenvalues			1.117
Sum of all canonical eigenvalues			0.249

Monte Carlo permutation test:

	First axis	Overall test
F - ratio	1.13	1.03
P - value	0.87	0.40

by the first two canonical axes. In the CCA, replicates of most treatments were clustered together, with the dry season autumn and winter burns separate from the wet season spring and summer burns along the first axis. Based on a Monte Carlo permutations test, however, these patterns were not supported on both the first CCA axis, or by the overall test of the species-environment relationship ($P > 0.05$).

INTERMEDIATE DISTURBANCE HYPOTHESIS:

At both 1m^2 and 100m^2 species richness in the autumn and winter burns increased with decreasing fire frequency (Figures 4.6 and 4.7). Species richness under spring burning, however, decreased with fire frequency at 1m^2 and showed no change at 100m^2. Unlike the spring burn, species richness in the autumn and winter burns appeared as though it may peak at intermediate burn frequencies. Yet, due to the narrow range of burn frequencies, such a conclusion was only weakly supported.

HETEROGENEITY:

The slopes of the species/area regression were shallowest in the biennial and annual winter and annual spring burn treatments but these treatments also had the highest y-intercepts (Table 4.3.). The steepest slopes, but lowest y-intercepts, were recorded for the fire protection, annual autumn, biennial spring hot and quinquennial spring burns. When slopes were compared between treatments, the majority of combinations with the annual autumn burn were excluded due to insufficient homogeneity of slope (Figure 4.8). Where the slopes for treatments were significantly different from each other ($P < 0.05$), the majority included comparisons with the fire protection, or annual spring and biennial winter burn treatments. These represented the treatments with the highest and lowest slopes, respectively (Table 4.3).

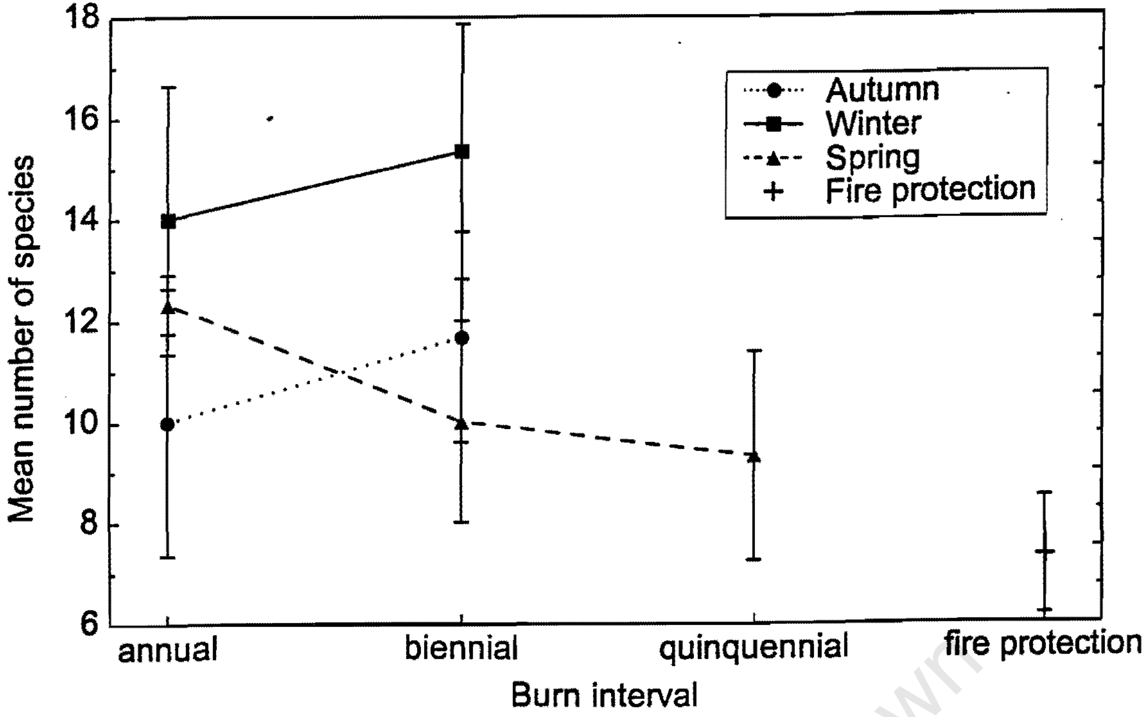


Figure 4.6. Effect of burn frequency on species richness, sampled in different seasons of burn at 1m^2 in the Cathedral Peak Brotherton trial.

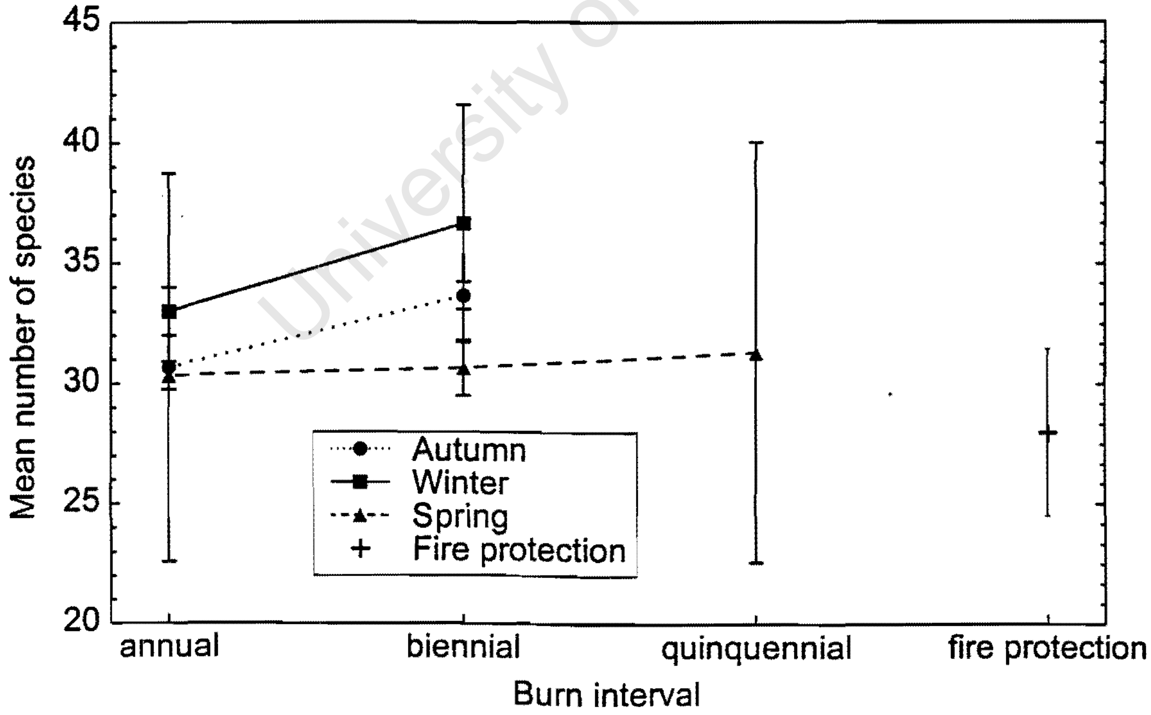


Figure 4.7. Effect of burn frequency on species richness, sampled in different seasons of burn at 100m^2 in the Cathedral Peak Brotherton trial.

DISSIMILARITY COMPARISONS:

Species turnover within treatments, measured by the Percentage dissimilarity between their replicates, was lowest in the biennial summer and annual spring burns, and highest for the quinquennial burn treatment (Table 4.4). In comparisons of the dissimilarity in species composition between treatments, the burn treatments were more similar to each other than to the fire protection treatment (Figure 4.9). Quinquennial spring burn and annual autumn burn treatments yielded the next highest dissimilarities. In testing the degree to which fire treatments were determining the species composition of the treatments, only replicates of the annual autumn, biennial spring hot and quinquennial spring burns differed more to each other than to replicates of other treatments. Replicates of the remaining treatments were significantly more similar to each other than to replicates of other treatments ($P < 0.01$).

BETA DIVERSITY:

Standardised beta diversity showed weak trends according to burn frequency (Table 4.5). Except for catchment IX, the longer fire return intervals (octennial burn and fire protection in catchment XV) were more heterogeneous than the biennial burn treatments. The fire protection treatment in catchment IX, however, was marginally less heterogeneous than its fire-break. Within the biennial treatments, the winter and spring burns displayed little additional heterogeneity to their fire-breaks. The biennial summer and autumn treatments, however, nearly matched the standardised dissimilarity produced by the octennial spring burn.

Dissimilarity between catchment and fire-break pairs poorly matched the patterns in standardised beta diversity (Table 4.5). However, catchment X (biennial spring burn), which had a very low standardised heterogeneity, also

Table 4.3. Regression estimates for species/area curves in the Cathedral Peak Brotherton trial; $y = a+bx+eps$; y = logarithm of the number of species; x = logarithm of area in m^2; a = Y-intercept; b = slope.

Burn treatments	Y-intercept	Slope	R^2
Biennial summer	1.086	0.247	0.965
Annual autumn	0.985	0.235	0.751
Biennial autumn	1.080	0.188	0.916
Annual winter	1.176	0.188	0.891
Biennial winter	1.182	0.186	0.905
Annual spring	1.103	0.263	0.950
Biennial spring	0.985	0.254	0.931
Biennial spring Hot	0.987	0.254	0.817
Quinquennial spring	0.964	0.289	0.699
Fire protection	0.860	0.247	0.950

	2y Sum	1y Aut	2y Aut	1y Win	2y Win	1y Spr	2y Spr	2y Spr H	5y Spr	FP
2y Sum										
1y Aut	–									
2y Aut		–								
1y Win	★	–								
2y Win	★	–								
1y Spr	★	–	★							
2y Spr		–			★	★				
2y Spr H	–				★	★	–			
5y Spr										
FP		–	★	★	★	★		–	–	

Figure 4.8. Comparison of the slopes of species/area regressions between burn treatments in the Cathedral Peak Brotherton trial.

– comparisons excluded due to significantly different ($P < 0.05$) F-Max values.

★ slopes significantly different ($P < 0.05$).

Table 4.4. Mean Percentage dissimilarity in the species composition between replicates (sampled at $100m^2$) of each treatment in the Cathedral Peak Brotherton trial.

Burn treatments	Percentage dissimilarity
Biennial summer	31.18
Annual autumn	42.50
Biennial autumn	35.07
Annual winter	27.57
Biennial winter	38.27
Annual spring	33.34
Biennial spring	37.84
Biennial spring Hot	43.23
Quinquennial spring	51.61
Fire protection	45.74

	2y Sum	1y Aut	2y Aut	1y Win	2y Win	1y Spr	2y Spr	2y Spr H	5y Spr	FP
2y Sum										
1y Aut	40.19									
2y Aut	34.67	38.36								
1y Win	33.75	33.60	31.99							
2y Win	36.83	40.21	34.85	34.34						
1y Spr	33.81	40.49	35.20	34.13	37.74					
2y Spr	37.00	42.03	37.98	37.16	39.94	37.46				
2y Spr H	36.19	44.54	39.95	37.17	41.41	39.80	39.84			
5y Spr	43.09	51.27	47.33	47.98	47.18	46.16	44.83	48.36		
FP	53.38	58.65	59.76	58.54	57.80	56.81	55.15	55.12	50.28	

Figure 4.9. Percentage dissimilarity in the species composition between treatments of the Cathedral Peak Brotherton trial; calculated as the mean dissimilarity between the replicates (sampled at $100m^2$) of the treatments being compared.

Table 4.5. Percentage dissimilarity of the species composition in the burn treatments of the Cathedral Peak catchments and their adjoining annually burnt fire-breaks, each sampled using ten belt transects (4m x 25m) paired in the catchment and fire-break.

Burn treatment	Catchment number	Percentage dissimilarity in the:		Difference between the dissimilarity in the Catchment and Fire-break	Percentage dissimilarity between transect pairs:	
		Catchment	Fire-break		Mean	Standard deviation
Biennial summer	VIII	45.64	37.30	8.34	43.34	9.24
Biennial autumn	VI	43.98	36.70	7.28	36.57	6.09
Biennial winter	I	44.77	42.22	2.55	43.20	9.89
Biennial spring	X	36.83	36.70	0.13	28.57	4.72
Octennial spring	XIII	40.88	31.53	9.34	58.02	8.99
Fire protection	IX	46.65	46.94	-0.29	40.87	4.57
Fire protection	XV	43.34	31.46	11.88	49.67	8.80

	2y Sum *C* VIII	2y Aut *C* VI	2y Win *C* I	2y Spr *C* X	8y Spr *C* XIII	FP *C* IX	FP *C* XV
2y Sum *C* VIII							
2y Aut *C* VI							
2y Win *C* I							
2y Spr *C* X	★		★				
8y Spr *C* XIII	★	★	★	★			
FP *C* IX				★	★		
FP *C* XV		★		★			

Figure 4.10. Comparisons of the Percentage dissimilarity between catchments (*C*) at Cathedral Peak, sampled as the mean dissimilarity in species composition in ten pairs of block transects (4m x 25m) in the burn treatment of each catchment and its adjoining annually burnt fire break, compared using a Tukey HSD MANOVA.

★ treatment were significantly different (*P* <0.05).

Table 4.6. Species richness of the burn treatments in the Cathedral Peak catchments (*C*) compared to their adjoining annually burnt fire-breaks (*FB*), sampled from ten pairs of block transects (4m x 25m) at each catchment/fire-break interface, where: *TP* = the total number of species in a transect pair,

$$\bar{x} = \frac{1}{n}\sum_{i=1}^{n}\left(\frac{x_i}{TP}\times\frac{100}{1}\right) \text{ and } S_x = \sqrt{\Sigma\left(\frac{x_i}{TP}\times\frac{100}{1}\right)^2 - \frac{1}{n}\left(\Sigma\,\frac{x_i}{TP}\times\frac{100}{1}\right)^2 \Big/ (n-1)}$$

Burn treatment	Catchment number	Mean number of species in:			$\bar{x}$ and S_x where x = number of species common to both *C* and *FB* in a transect pair		$\bar{x}$ and S_x where x = number of species in a transect pair that was unique to:			
		C	*FB*	*TP*			*C*		*FB*	
Biennial summer	VIII	18.4	23.8	30.1	40.0	9.1	21.0	9.8	39.0	7.0
Biennial autumn	VI	23.9	30.3	36.9	46.6	6.3	17.8	5.2	35.6	4.1
Biennial winter	I	22.8	29.9	37.5	40.3	9.7	20.0	9.9	39.7	12.7
Biennial spring	X	29.6	26.2	35.8	55.7	5.8	26.9	4.5	17.4	6.0
Octennial spring	XIII	21.9	31.4	42.0	26.9	7.3	25.0	5.5	48.1	7.2
Fire protection	IX	26.8	27.3	38.0	42.1	4.7	28.5	5.9	29.4	5.7
Fire protection	XV	18.8	20.8	29.6	34.5	7.9	30.6	5.6	35.9	9.2

had the most similar species composition to its adjoining fire-break. Excluding the octennial burn treatment, dissimilarity between the transect pairs of the remaining treatments did not differ significantly (*P* >0.05) (Figure 4.10). This contrasted with the range of standardised heterogeneity values displayed by these treatments (Table 4.5). The octennial burn differed the most from its adjacent fire-break, complementing its high beta diversity. All significantly different comparisons (*P* <0.05) between catchments, of the dissimilarity between transect pairs, included combinations with the biennial and octennial spring burns (Figure 4.10).

This difference between the biennial and octennial spring burn catchments was not evident in the percentage of species that were unique to the catchment (Table 4.6). However, the percentage of species unique to the fire-break showed a closer relation to the dissimilarity in transect pairs for these two catchments. The inverse of this was displayed by the proportion of species common to both the catchment and fire-break in the transect pairs.

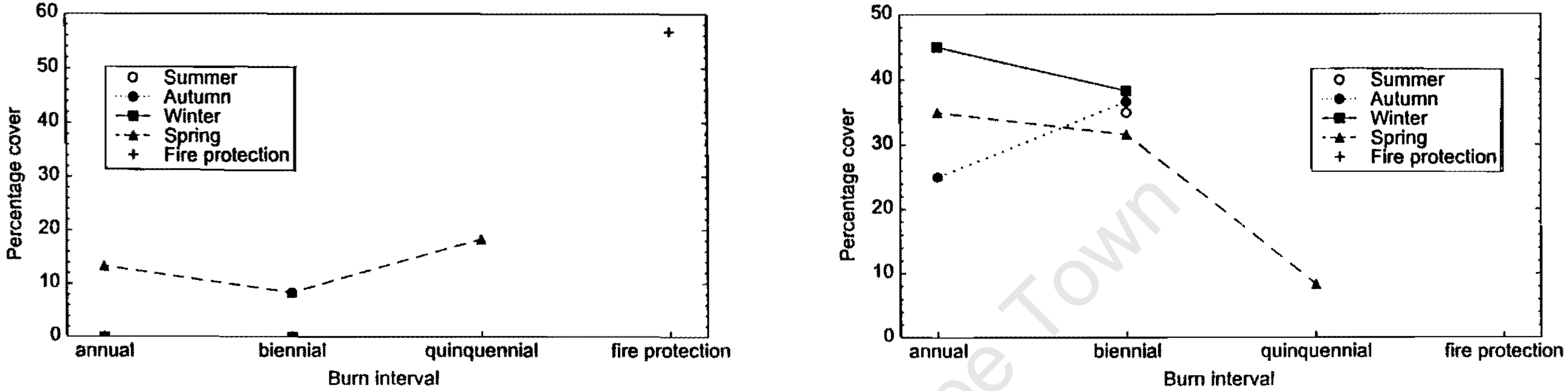
SWARD ATTRIBUTES:

PERCENTAGE COVER:

Aerial cover of the plots sampled in the Brotherton trial was largely dominated by two bunch grass species *Koeleria capensis* and *Themeda triandra* (Table 4.7). The percentage cover constituted by these two grasses increased with burn frequency and was higher in winter than spring (Figures 4.11).The only forbs recorded in the percentage aerial cover, *Helichrysum aureonitens*, *Lotononis lotononoides* and *Senecio harveianus* were present across the site, but seldom in large enough quantities to merit inclusion in the measurement of percentage cover. Like the forbs, the grasses, *Heteropogon contortus* and *Monocymbium ceresiiforme* occurred throughout the trial but only in high

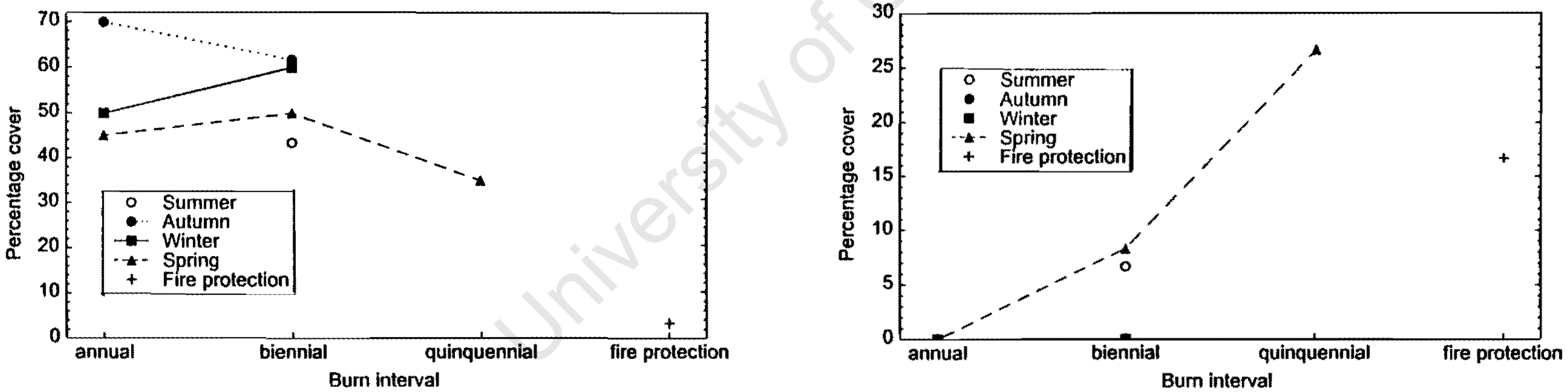
Table 4.7. Percentage cover estimates, averaged from the three replicates of each treatment in the Cathedral Peak Brotherton trial.

		2y Sum	1y Aut	2y Aut	1y Win	2y Win	1y Spr	2y Spr	2y Spr H	5y Spr	FP
Forbs	*Helichrysum aureonitens*	3.3	0	0	0	0	0	0	0	0	5
	Lotononis lotononoides	0	0	0	0	0	3.3	0	0	0	0
	Senecio harveianus	0	0	0	0	0	0	0	0	0	13.3
Grasses	*Andropogon appendiculatus*	1.7	1.7	0	0	0	1.7	0	15	5	1.7
	Diheteropogon amplectens	1.7	3.3	1.7	3.3	0	1.7	0	0	0	0
	Harpochloa falx	8.3	0	0	0	0	13.3	8.3	5	18.3	56.7
	Heteropogon contortus	0	0	0	1.7	0	0	0	0	0	0
	Koeleria capensis	35	25	36.7	45	38.3	35	31.7	33.3	8.3	0
	Monocymbium ceresiiforme	0	0	0	0	1.7	0	0	0	0	0
	Stiburus conrathii	0	0	0	0	0	0	1.7	3.3	6.7	3.3
	Themeda triandra	43.3	70	61.7	50	60	45	50	40	35	3.3
	Tristachya leucothrix	6.7	0	0	0	0	0	8.3	3.3	26.7	16.7



Harpochloa falx

Koeleria capensis



Themeda triandra

Tristachya leucothrix

Figure 4.11. Effect of frequency and season of burn, after 18 years of continuous treatment, on the species that dominated the aerial cover of the Cathedral Peak Brotherton trial.

enough proportions to be recorded for a single treatment each. The grasses *Andropogon appendiculatus*, *Diheteropogon amplectens* and *Stiburus conrathii* also occurred throughout the trial, but mostly at densities below or at the five percent minimum. The two sod-forming species, *Harpochloa falx* and *Tristachya leucothrix*, both increased as burn frequency decreased, the former being the dominant species in the fire protection treatment. Both species also only responded to spring and summer burning (Table 4.7 and Figure 4.11).

LIGHT ATTENUATION:

At the top of the sward, there was no difference in F irrespective of the spring burn treatment (Figure 4.12). Moving down the sward, the F values for the burnt quinquennial spring burn replicate were the same as those from the annual burn. In the two unburnt quinquennial spring burn replicates, however, the F increased dramatically down the sward. Below 200mm above the ground the F of these replicates increased substantially, to the point where the F was five times greater than in the annual and burnt quinquennial burn replicate at ground level.

BIOMASS:

Biomass in the autumn burns of the Brotherton trial decreased between the annual and biennial treatments (Figure 4.13). Average biomass did not differ significantly between the annual and biennial winter burn treatments, but definitely increased in the spring burns with decreasing burn frequency. Though biomass in the annual burn treatments differed according to the season of burn, there was little difference between the biennial burn treatments.

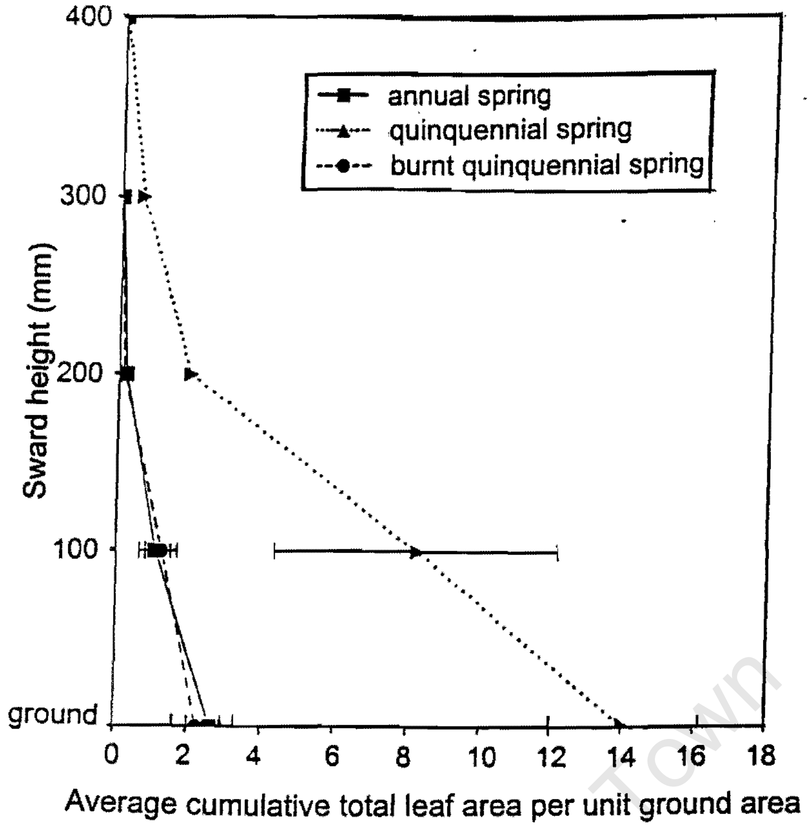


Figure 4.12. Effect of burn frequency on light attenuation down the sward in the Cathedral Peak Brotherton trial, averaged from ten sets of readings in each replicate of the shortest and longest spring burn treatments.

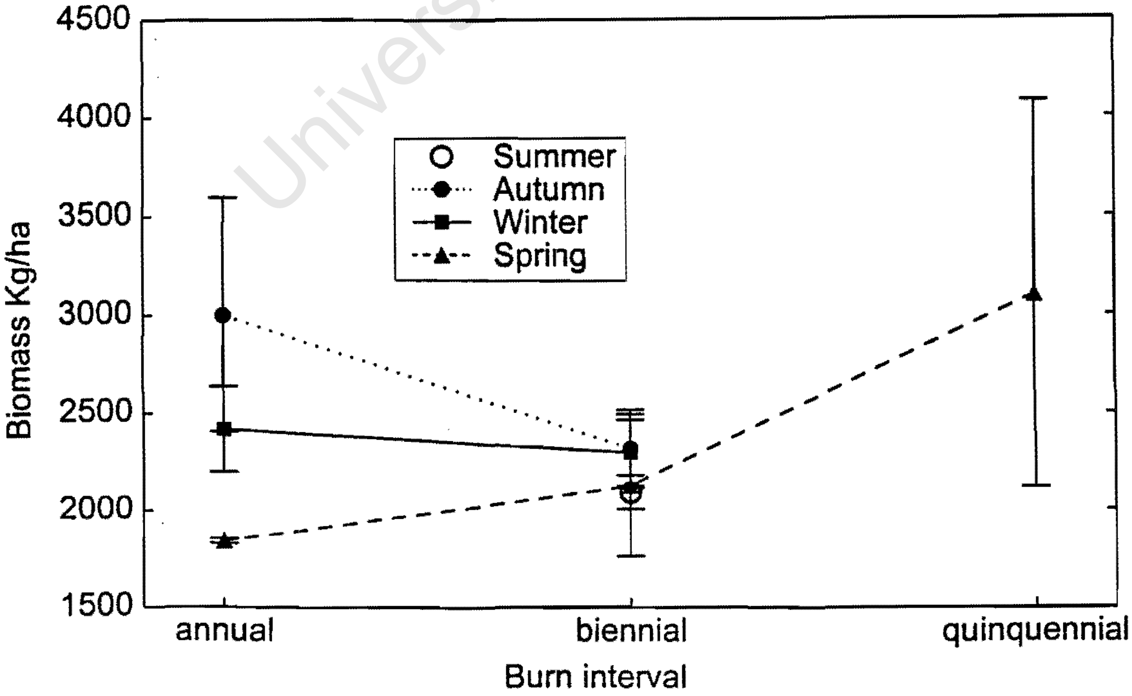


Figure 4.13. Influence of frequency and season of burn on sward biomass in the Cathedral Peak Brotherton trial.

4.5 DISCUSSION

THE EFFECT OF FREQUENCY AND SEASON OF BURN:

Total species richness in each of the treatments that were sampled, showed no clear trends across frequency or season of burn (Table 4.1). Taken as the mean of the three replicates in each treatment, however, the winter and autumn treatments suggested that species richness may peak at intermediate fire frequencies, at both 1m^2 and 100m^2 (Figures 4.6 and 4.7). Similar conclusions were drawn by Morris, Dicks, Everson and Everson (1999) from work previously done on the trial. Due to the narrow range of burn frequencies available in this trial, and the varied response to spring burning at different scales of measurement, predictions of the IDH could not be fully supported. The narrow range of burn frequencies and differences between the burn seasons also precluded any clear trends being determined for the response of biomass to burn frequency (Figure 4.13). In addition to the frequency and season of burn the biennial spring treatments had been manipulated as high (hot) and low intensity (cold) burns. Measures of their alpha diversity, however, showed no significant differences between them.

BURNING VERSUS FIRE PROTECTION:

Like the other two sites, ordination of the species abundance data provided evidence for directional changes in species composition with fire protection (Figure 4.3). Differences between the burn treatments and the fire protection treatment were also supported by the measures of dissimilarity in species composition between treatments (Figure 4.9). In the quinquennial spring treatment, one of the three replicates had been accidentally burnt a year prior to sampling and to its scheduled burn. The similarity in sward structure between the burnt quinquennial replicate and the annual spring burn treatment, as opposed to the unburnt quinquennial replicates, indicated that post-burn succession was having a greater effect on sward structure than long term effects of fire frequency (Figure 4.12). The differences in post-burn age between the replicates also accounts for the high proportion of rare species recorded for the quinquennial spring treatment (Table 4.2). The fire protection treatment, however, had not been burnt for 18 years, implying that directional succession was accounting for its high proportion of rare species, especially those unique to the treatment.

RESPONSES TO BURNING:

As for Ukulinga and Honeydale, the cover represented by the dominant grass species showed clear trends according to frequency and season of burn (Figure 4.11). One of the dominant bunch grass species found to increase with burn frequency, *Koeleria capensis*, is a C_3 species. This was interesting, as the responses of grass cover to frequency and season of burn that have previously been shown, were mostly for the C_4 species that dominate the southern African grassland biome, C_3 species only occurring at high altitudes (O'Connor & Bredenkamp 1997). Previous work at Cathedral Peak also indicated that the dominant bunch grass species increased and sod-forming species decreased with increasing burn frequency (Granger 1976; Everson & Tainton 1984; Everson *et al.* 1988). Interestingly, the sod-forming species were only favoured by burning during the growing season or by fire protection. Again, forbs were poorly represented in the cover and showed no clear response to burning treatments. This was supported by the ordination indicating that environmental gradients across the site were overriding the effects of frequency and season of burn on species composition (Figure 4.4). The distribution of species and rare species across the replicates of the treatments was, however, less dispersed than at Ukulinga (Tables 4.1 and 4.2). In addition, in most of the treatments, the replicates were more similar to each other than to replicates of other treatments. This implied that environmental gradients were not having as marked an effect as at the other two sites. Nonetheless, there were no clear trends in proportionate representation of each treatment's species complement in its replicates (Table 4.1) or the within treatment dissimilarity comparisons (Table 4.4). This supported the ordination results, by suggesting that the frequency and season of burn were not determining the degree of similarity between the replicates of each treatment. As species composition did not appear to have been influenced by the frequency or season of burn , the absence of clear trends in vegetation patchiness was to be expected (Table 4.3). Comparisons of vegetation patchiness between treatments showed that the burn treatments were more similar to each other than to the fire protection treatment (Figure 4.8). This implied a directional change in patchiness with fire protection.

BETA DIVERSITY:

Few studies have examined the effects of disturbance on changes in species composition across a landscape (beta diversity). To examine beta diversity in the Cathedral Peak catchments, it was first necessary to account for the differences between catchments. This was done by comparing the beta diversity in the catchments to that in the annually burnt fire-breaks that formed the boundaries of each catchment. Standardised according to the beta diversity of their fire breaks, the weak pattern shown in the catchments suggested that infrequent burning promoted vegetation patchiness at a landscape level (Table 4.5). Seasonal differences in the biennial burns also implied that burning towards the end of the growing season in summer and autumn increased heterogeneity. However, the small plot trials at each site did not support this effect of burn season (Tables 2.3, 3.3 and 4.3). The negative standardised beta diversity recorded for catchment IX was not considered to be a true reflection of the effects of fire protection in this treatment. Though the vegetation in this catchment has shown a marked directional succession to include woody species (Granger 1976), the catchment has been burnt several times since it was initiated in 1952. Thus catchment IX was not a complete fire protection treatment. Rather, burning appears to have resulted in the vegetation, at least on the catchment boundary, having a similar patchiness to that in the fire-break.

For burning to influence vegetation heterogeneity, it must first influence species composition. Therefore, the species composition of the annually burnt fire breaks should have been more similar to the biennial, rather than the octennial, burn treatments. In the comparisons between the transect pairs in each catchment, this was the case (Table 4.5 and Figure 4.10). The number of species common to the catchment and fire-break indicated that longer burns favoured more different species to the fire-breaks than the biennial treatments were (Table 4.6). The highest proportions of species unique to the catchments occurred under fire protection, also suggesting that directional changes in species composition were occurring in the absence of disturbance.

SUMMARY:

So, although there was some support for the IDH, the range of burning frequencies was not great enough. This narrow range of fire frequencies also made interpreting the effect of burning regimes on biomass difficult. The species composition of the burn treatments appeared to be responding to environmental gradients rather than the burn treatments. Further, species composition differed between the burn and fire protection treatments, indicating directional changes in composition with fire protection. Instead of long term effects of burn frequency, post-burn changes were found to determine sward structure. Like the other two sites, cover was dominated by a few grass species that were clearly responding to frequency and season of burn. Though no effect could be determined according to the burn season, vegetation patchiness at a landscape showed a marginal increase with fire protection.

GENERAL

5.1 INTRODUCTION

Vegetation patterns, in particular sward productivity, across the southern African grasslands have shown positive relations to the rainfall gradient across the biome (O'Connor & Bredenkamp 1997). Southern African grasslands can also be divided into two groups (dry and moist) according to whether they fall above or below the 625mm isohyet (Rutherford & Westfall 1994). In the dry grasslands, "sweet", palatable grasses predominate (O'Connor & Bredenkamp 1997), commencement of growth is determined by moisture availability (Danckwerts 1984) and active growth is restricted to short sporadic periods following rainfall events (Danckwerts 1988). "Sour" grasses that are unpalatable in winter, predominate the moist grasslands (O'Connor & Bredenkamp 1997), where commencement of growth depends on soil temperatures (Leigh 1960; Steinke & Nel 1967; Rethman & Booysen 1969; Everson & Everson 1987), and growth is almost continuous, but at a variable rate (Everson 1985).

However, in addition to rainfall, productivity is also influenced by the sward composition, the availability of nitrogen and phosphorus and temperature variations across the biome (O'Connor & Bredenkamp 1997). The Drakensberg mountains, in particular, are prone to winter frosts that kill off the above-ground parts of the grasses. Further, the distribution of rainfall and the length of the dry season limit vegetation growth in the region (Everson 1994). Therefore to gain some idea of the effect of fire on grassland phytodiversity, it was necessary to examine sites that were widely spread across the biome. Many of the burning trials that were initiated at one time or another in the grassland biome have not been maintained. However, the three remaining trials that were sampled in my study were widely spread across the biome and represented both dry and moist, plus lowland and montane grasslands.

In an attempt to generalise diversity patterns across the grassland biome, the relationship between biomass and species richness was examined in the three study sites. Due to productivity responding to factors other than rainfall, biomass was calculated from direct measurements at each site in addition to being estimated from the general biomass/rainfall regression for the grassland biome (O'Connor & Bredenkamp 1997). In the absence of detailed floristic analyses of the southern African grasslands, the wide geographic range of the sites provided the opportunity to examine the occurrence of families and taxa across the biome. This also provided the opportunity to explore the basic biology of grassland forbs, particularly the distribution of underground storage organs of the forbs.

5.2 MATERIALS AND METHODS

BIOMASS AND SPECIES RICHNESS:

The presence of a humped-back relationship between the number of species (at 1m^2 and 100m^2) and biomass, for the grassland biome, was explored using the biomass data collected at the three sites studied. Biomass was calculated by mowing at Ukulinga, and by means of the disk pasture meter in the Honeydale camp 32 trial and the Cathedral Peak Brotherton trial. In addition, biomass for these three sites was calculated directly from measurements at the site and from the relationship across the grassland biome between mean annual rainfall and mean herbage yield. The biomass values calculated from the latter source were derived using the mean annual rainfall figures for each site and the afore mentioned relationship described by the linear regression:

$y = 3.72x - 742$ $(R^2 = 0.53; F = 19.0; P < 0.006)$

where: y = the mean herbage yield ($Kg.ha^{-1}$)

x = mean annual rainfall (mm)

(O'Connor & Bredenkamp 1997).

ANALYSIS OF THE FLORA:

Where possible, species from all the trials sampled in my study were identified and specimens collected. These were used to examine the plant families represented at each site and the types of underground organs favoured by the forbs sampled in the burning trials. Using Pooley (1998) and Batten and Bokelmann (1966) all the identifiable forbs which occurred in burn treatments and on which information could be found, were divided in to monocotyledonous and dicotyledonous plants, annuals and perennials and their underground organs classified. For the monocotyledonous plants, the underground organs were divided into bulbs, corms, rhizomes, tubers and other roots. As some dicotyledonous plants had combinations of wood rootstocks and tubers, these were combined and distinguished from other roots.

5.3 RESULTS

BIOMASS AND SPECIES RICHNESS:

Average biomass calculated from the burn plots was lowest at Cathedral Peak, intermediate at Ukulinga, and greatest at Honeydale (Table 5.1). Plotted against the average number of species recorded across the burn treatments of these trials, the potential for a humpbacked curve was shown at $1m^2$ and $100m^2$ (Figures 5.1 and 5.2). When biomass was calculated from the linear relationship between biomass and rainfall across the grassland biome, the pattern of biomass across the sites was reversed (Figures 5.3 and 5.4).

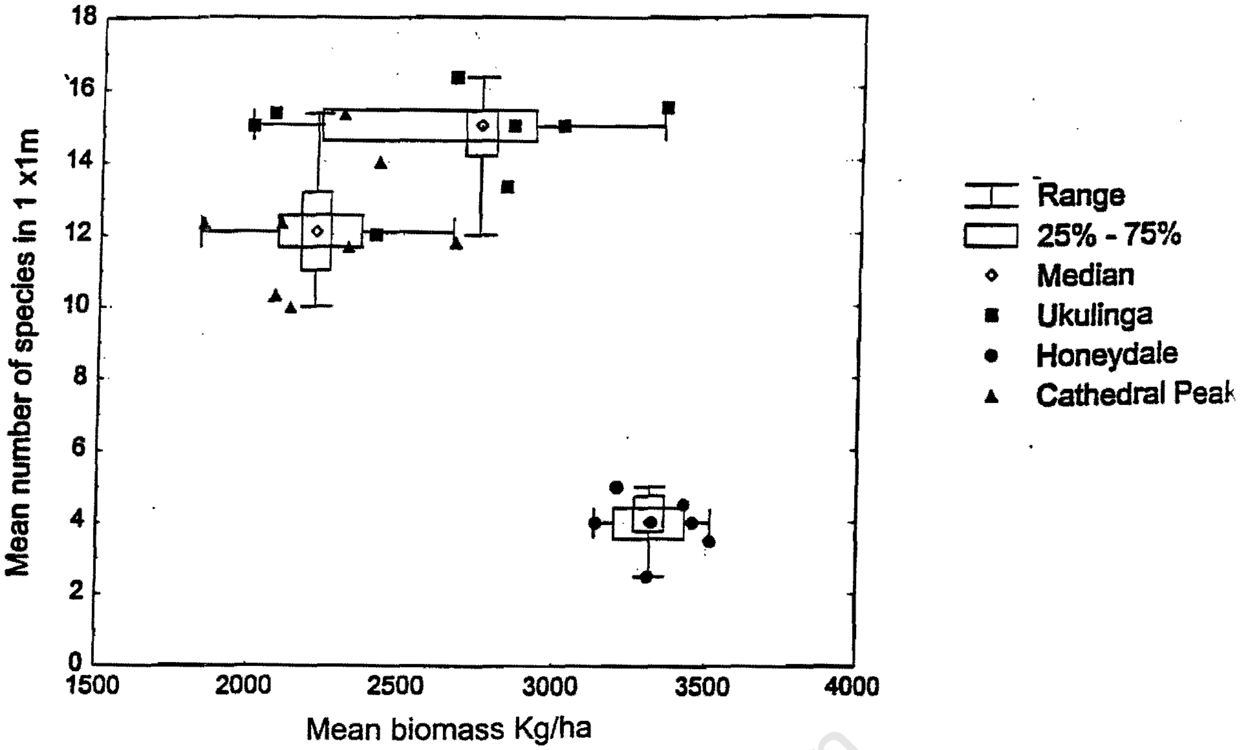


Figure 5.1. Relationship between species richness (sampled at 1m^2) and the biomass calculated for each site.

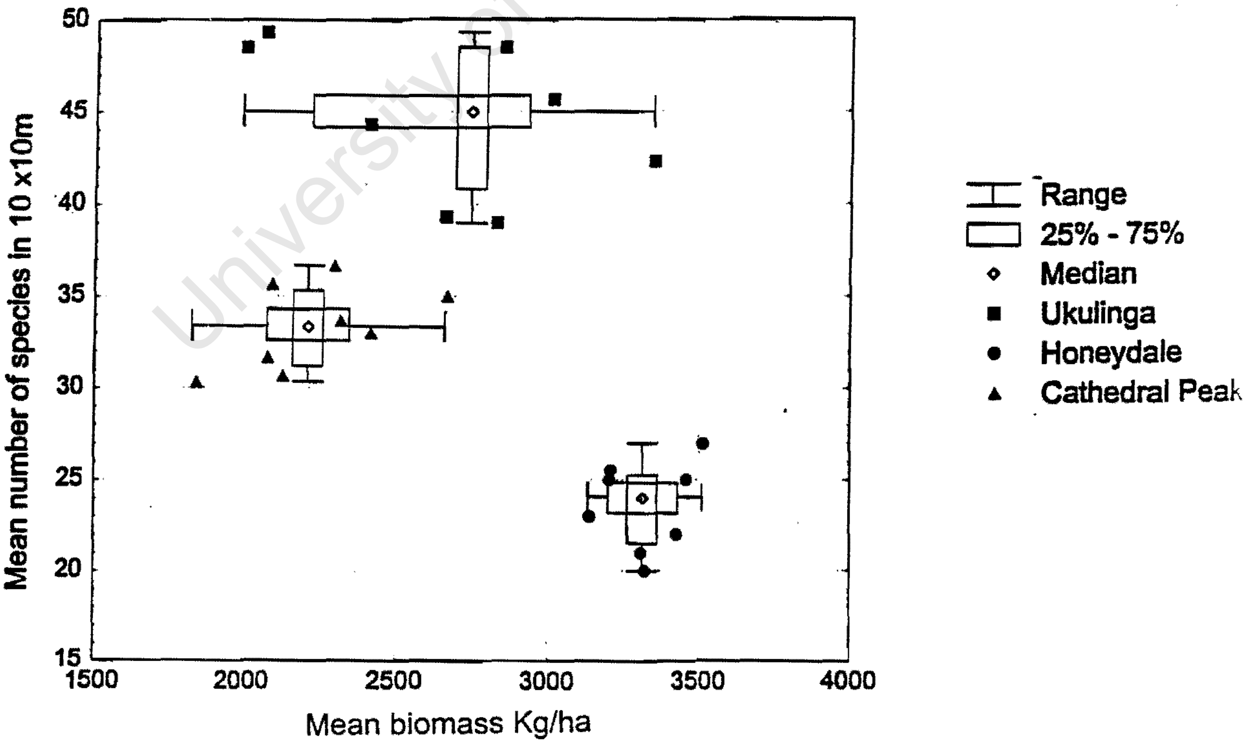


Figure 5.2. Relationship between species richness (sampled at 100m^2) and the biomass calculated for each site.

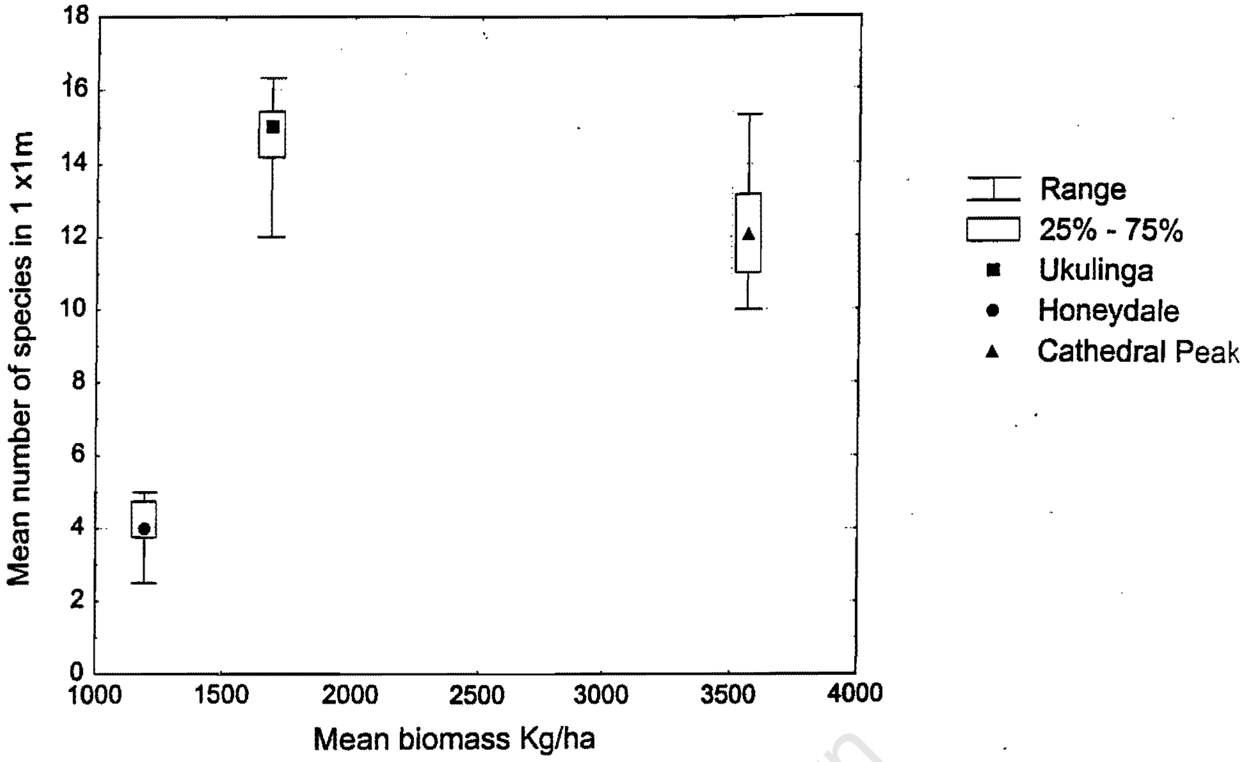


Figure 5.3. Relationship between species richness (sampled at $1m^2$) and the biomass, calculated for each site from the regressed relationship between rainfall and biomass across the grassland biome.

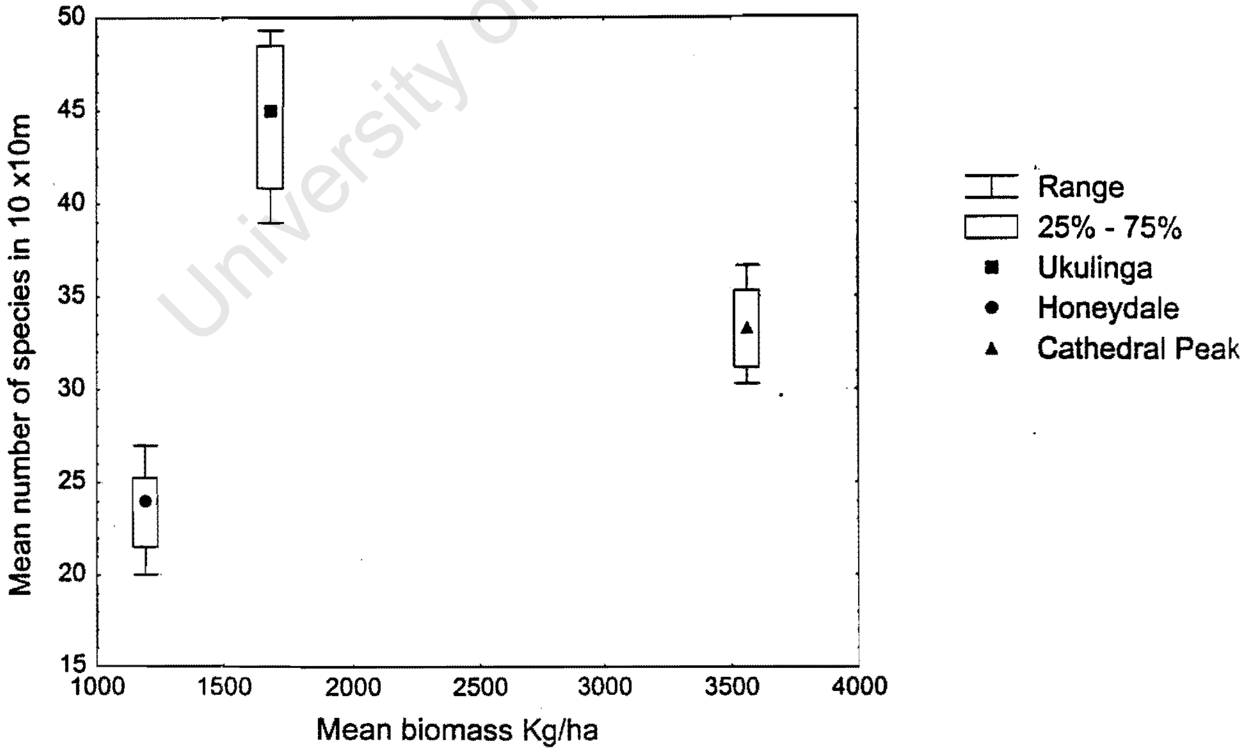


Figure 5.4. Relationship between species richness (sampled at $100m^2$) and the biomass, calculated for each site from the regressed relationship between rainfall and biomass across the grassland biome.

Calculated in this fashion, Cathedral Peak had the highest biomass and Honeydale the lowest. The mean number of species at 1m^2 and 100m^2 plotted for the three sites against this measure of biomass also showed the potential to fall along a humpbacked curve.

Table 5.1 Median values for the relation between biomass and species richness.

Site	Biomass (Kg.ha^{-1}) calculated from: Disk pasture meter readings	Regressed relationship between rainfall and biomass	Species richness in: 1m^2	100m^2
Ukulinga	2738.5	1683.1	15	45
Honeydale	3311.5	1191.0	4	24
Cathedral Peak	2213.1	3565.8	12.1	33.3

ANALYSIS OF THE FLORA:

TAXA BY FAMILY:

Not only were the grasses shown to dominate the aerial cover of the plots, but the family also consistently had one of the highest species counts rivalled only by the Asteraceae (Table 5.2). The Asteraceae were largely composed of *Senecio* and *Helichrysum* species. Each of these two genera represented roughly a third of the Asteraceae species at each site. Genera in the Poaceae, however, were seldom represented by more than one species. The strong representation of the Fabaceae at Ukulinga was partly due to the trees in the fire protection treatments. Many of the remaining species from this family had a creeping growth form. Like the grasses, sedges (family Cyperaceae) were present at each site. Though there were few sedge species, they were fairly common at each site. Orchid species (family Orchidaceae) were fairly common at Ukulinga and Cathedral Peak, but were not recorded in the drier Honeydale plots. Showing a similar pattern of species abundance were the

Families	Ukulinga burning / mowing trial		Honeydale camp 32 trial		Cathedral Peak Brotherton trial	
	No. spp.	% spp.	No. spp.	% spp.	No. spp.	% spp.
Poaceae	19	13.5	14	20	19	21.3
Asteraceae	18	12.8	7	10	25	28.1
Fabaceae	17	12.1	2	2.9	1	1.1
Orchidaceae	4	2.8	0	0	5	5.6
Cyperaceae	4	2.8	2	2.9	2	2.2
Rubiaceae	6	4.3	0	0	3	3.4
Hyacinthaceae	5	3.5	2	2.9	0	0
Hypoxidaceae	4	2.8	1	1.4	2	2.2
Asclepiadaceae	2	1.4	0	0	4	4.5
Commelinaceae	2	1.4	2	2.9	1	1.1
Iridaceae	4	2.8	0	0	2	2.2
Malvaceae	1	0.7	3	4.3	0	0
Scrophulariaceae	3	2.1	1	1.4	1	1.1
Lamiaceae	4	2.8	1	1.4	0	0
Campanulaceae	1	0.7	0	0	3	3.4
Convolvulaceae	1	0.7	2	2.9	0	0
Acanthaceae	3	2.1	1	1.4	0	0
Gentianaceae	1	0.7	1	1.4	1	1.1
Oxalidaceae	1	0.7	1	1.4	1	1.1
Sterculiaceae	1	0.7	1	1.4	1	1.1
Clusiaceae	1	0.7	0	0	2	2.2
Verbenaceae	2	1.4	1	1.4	0	0
Euphorbiaceae	2	1.4	0	0	1	1.1
Selaginaceae	0	0	1	1.4	1	1.1
Oleaceae	1	0.7	1	1.4	0	0
Tiliaceae	1	0.7	1	1.4	0	0
Crassulaceae	1	0.7	0	0	1	1.1
Polygalaceae	1	0.7	0	0	1	1.1
Dipsacaceae	2	1.4	0	0	0	0
Geraniaceae	2	1.4	0	0	0	0
Asparagaceae	0	0	1	1.4	0	0
Asphodelaceae	0	0	1	1.4	0	0
Cactaceae	0	0	1	1.4	0	0
Celastraceae	0	0	1	1.4	0	0
Curcubitaceae	0	0	1	1.4	0	0
Ebenaceae	0	0	1	1.4	0	0
Lobeliaceae	0	0	1	1.4	0	0
Solanaceae	0	0	1	1.4	0	0
Ericaceae	0	0	0	0	1	1.1
Ophioglossaceae	0	0	0	0	1	1.1
Ranunculaceae	0	0	0	0	1	1.1
Rosaceae	0	0	0	0	1	1.1
Valerianaceae	0	0	0	0	1	1.1
Adiantaceae	1	0.7	0	0	0	0
Amaryllidaceae	1	0.7	0	0	0	0
Anacardiaceae	1	0.7	0	0	0	0
Araceae	1	0.7	0	0	0	0
Caryophyllaceae	1	0.7	0	0	0	0
Eriospermacaceae	1	0.7	0	0	0	0
Meliaceae	1	0.7	0	0	0	0
Passifloraceae	1	0.7	0	0	0	0
Rhamnaceae	1	0.7	0	0	0	0
Rutaceae	1	0.7	0	0	0	0
Santalaceae	1	0.7	0	0	0	0
Urticaceae	1	0.7	0	0	0	0
Vitaceae	1	0.7	0	0	0	0
Unknowns	14	9.9	17	24.3	7	7.9
Number of species at site	141		70		89	

Table 5.2. Number and percentage of taxa per family from the burn plots at each site, arranged according to their proportional abundance.

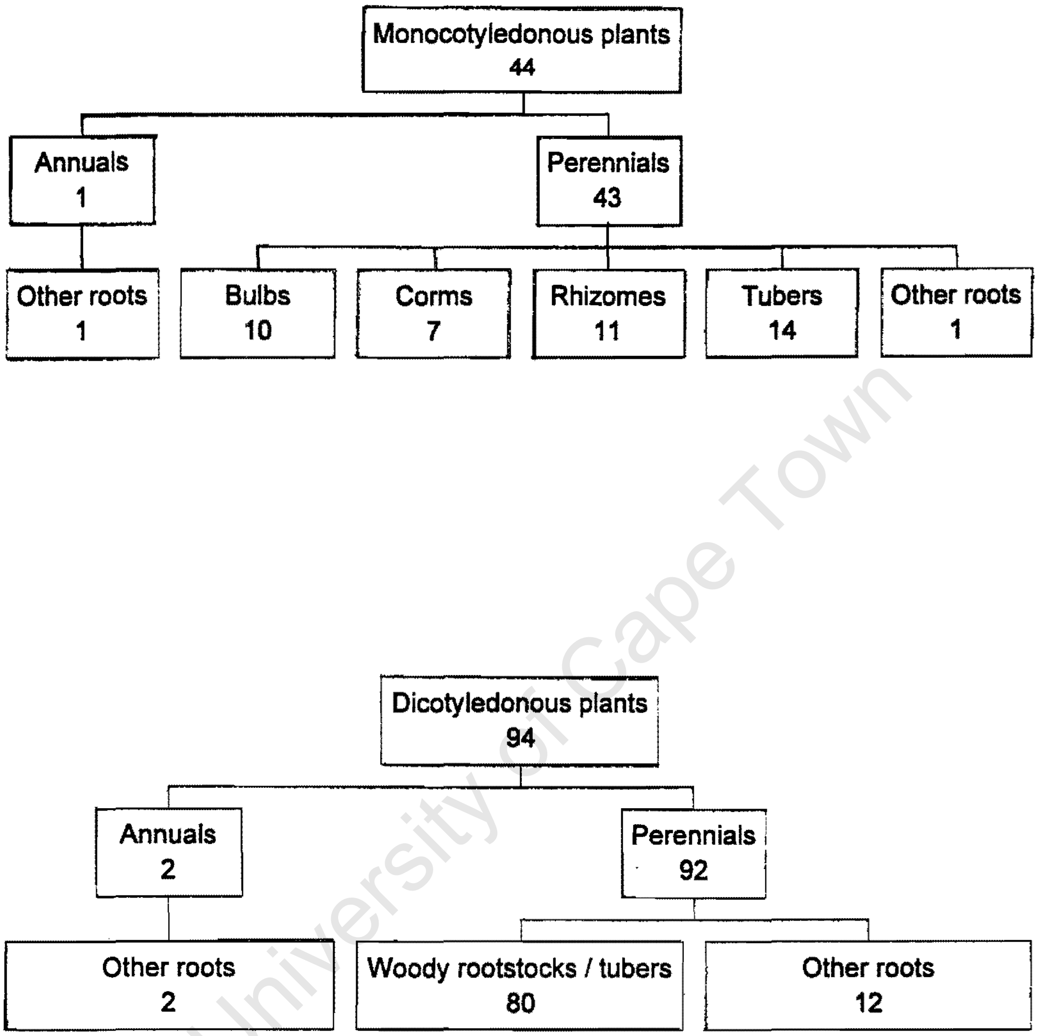


Figure 5.5. Breakdown of the underground structures of the forbs, sampled in the burning treatments from the three study sites, on which information could be found.

Rubiaceae, which like the Orchidaceae, were absent from the Honeydale plots. Other than the Hyacinthaceae, Hypoxidaceae, Iridaceae and Lamiaceae at Ukulinga and Asclepiadaceae, the remaining families were represented by few species at each site

FORB MORPHOLOGY:

From the identifiable forbs collected at the three study sites, there were more than twice as many dicotyledonous species as monocotyledonous species (Figure 5.5). Both monocots and dicots were represented almost entirely by perennial species. The majority of these species had some form of underground storage organs.

5.4 DISCUSSION

BIOMASS AND SPECIES RICHNESS:

With only three sites it was not possible to fit any form of regressed line to the relationship between productivity and species richness. However, species richness at the three study sites (at the $1m^2$ and $100m^2$ scale) showed peak richness at intermediate levels of biomass, consistent with studies in diverse vegetation types throughout the world (Al-Mufti *et al.* 1977; Grime 1979; Wheeler & Giller 1982; Bond 1983; Moore & Keddy 1989; Wisheu & Keddy 1989; Wheeler & Shaw 1991; Wilson & Shay 1990; Garcia *et al.* 1993; Rosenzweig & Abramsky 1993; Abrams 1995). Biomass was calculated both directly using the disk pasture meter and estimated from the linearly regressed relationship between mean annual rainfall and mean biomass across the grassland biome (O'Connor & Bredenkamp 1997). Regression estimates did not agree with measured biomass, perhaps because of local site conditions. In future studies, direct biomass readings need to be made on site at the same time that species richness is recorded.

To the best of my knowledge, this is the first report the presence of a humpbacked relationship between species richness and biomass in the southern African grassland biome. However, more data is required to generalise this trend across the grassland biome, and for this purpose the results of my study are provided in Table 5.1.

ANALYSIS OF THE FLORA:

TAXA BY FAMILY:

The majority of plant families present in the study sites were only represented by a few species each. Grasses not only dominated the aerial cover of the plots, but as a family were also well represented. However, unlike the other well represented family, the Asteraceae, the Poaceae were composed of a range of genera. The large proportion of creeping species in the Fabaceae at Ukulinga may have represented a growth form adapted to the tall grass sward. If shading were an issue, the ability to place photosynthetic organs above the moribund layer would be important. As this was not a common growth form in the other forbs, shading did not appear to determine plant growth form. Instead, as the sward ages, the results of my study suggest a change in species composition. It is believed that this change was from vernal to autumnal aspect forbs (Bayer 1955). However, this could not be quantified due to a lack of information on when forbs initiate growth and their flowering times.

FORB MORPHOLOGY:

One of the common traits of species in fire-prone environments is the presence of some form of underground storage organ, such as possessed by most of the forbs recorded in my study (Burtt-Davy 1922; Martin 1966; West 1971; Rourke 1972; McMaster 1976; Carlquist 1977). Based on the evidence submitted in Chapter 1.5, it is speculated that the grassland flora evolved under a variable fire regime. Fires would have occurred in different seasons and at irregular intervals, burning patches of varying size and intensity. Therefore, surviving grassland forbs are those that could cope with both frequent burning and extended periods between disturbances. When frequently burnt, the possession of storage reserves would allow these plants to resprout and flower after a burn. By producing photosynthetic organs soon after the fire, plants could replenish their storage reserves before they were outgrown and shaded by the grasses. In the absence of fire, insufficient warmth would reach the ground, and spring forbs may be prevented from resuming activity after their winter dormancy. If this continued for a number of years, it is predicted that the plants would expend their storage reserves, effectively being shaded out of the sward (Bayer 1955).

It seems likely that the lack of response by grassland forbs to frequency and season of burn may be due to their underground storage organs allowing them to tolerate a wide range of burning treatments. As the majority of burn treatments at each site coincided the year prior to this study, only the effects of the long term application of burning regimes could be tested. To examine post-burn succession, a range of treatments with different burn frequencies that coincide prior to their being burnt would be required. Further, there was no way of knowing whether directional succession under fire protection resulted in losses, as well as the addition of species. Some of the forbs may present, but dormant, in unburnt grasslands. To test this, fire protection treatments would have to be burnt, but as the trials used in my study were ongoing this was not possible.

SYNTHESIS

To examine the effects of different burning regimes on grassland phytodiversity, three long term burning trials were sampled. Widely located in the southern African grassland biome, east of the escarpment, results differed between sites. Trends across the sites, however, have provided general insights into the role of fire as a conservation management tool for the grassland biome.

THE EFFECT OF FREQUENCY AND SEASON OF BURN:

Whereas the total species richness in each treatment showed no clear trends according to either the frequency or season of burn at each site, species richness across the replicates of each treatment did. If species richness peaked at intermediate levels of disturbance, the IDH could be applied to maximise grassland biodiversity. This response, however, has received little attention in the southern African grasslands and fire-prone systems in general, with conflicting results where it was examined (Chapter 1.7). Though the autumn and winter burns from Cathedral Peak provided some support for the IDH, the predictions of the IDH could not be tested properly due to the narrow range of burn frequencies. At this site, the increase in species richness in the spring burns, with fire frequency at 1m^2, matched the results from the Scottish heathlands and South African Fynbos when sampled at the same scale (Hobbs *et al.* 1984; Schwilk *et al.* 1997). Like the study of the Fynbos, there was no support in the Cathedral Peak spring burns sampled at 100m^2 for the IDH. In addition, the similarity of the Honeydale results to those found in the North American tall grass prairies (Collins & Gibson 1990; Collins *et al.* 1995) and the absence of clear trends at Ukulinga, provided no evidence for the IDH in the fire-prone grasslands. However, because the burn treatments at each site had largely coincided, the effects of post-burn succession on species richness could not be tested. Therefore, only half of the predictions of the IDH have been examined in this study.

BIOMASS AND SPECIES RICHNESS:

This study also provided a first test for southern African grasslands of the humpbacked relationship between species richness and biomass, as demonstrated by a number of authors (Chapter 1.7). If such a relationship exists for the African grasslands, species richness could be predicted across the biome based on the biomass. As a linear relationship has already been shown between rainfall and biomass across the biome (O'Connor & Bredenkamp 1997), this was examined as a possible means of predicting biomass from rainfall. A humpbacked relationship between species richness and direct measures of biomass was supported by the results of my study, but biomass was not successfully predicted by rainfall. However, more data across the grassland biome is needed to test the generality of this potential relationship.

BURNING VERSUS FIRE PROTECTION:

Although there were no clear trends in alpha diversity, ordination showed that the species composition at each site differed between the burn treatments and fire protection treatment. As all the burn treatments at each site had roughly coincided the year prior to sampling, these differences implied a directional succession of species with fire protection. Such a directional succession has been widely reported across the southern African grassland biome, with either a turnover of grass species or grasses being replaced by herbaceous or woody species (Staples 1926, 1930; Glover & van Rensburg 1938; Edwards 1968; Roux 1969; Trollope 1974; Granger 1976; Robinson *et al.* 1979; Scotcher & Clarke 1981; Westfall, Everson & Everson 1983; Everson &

Tainton 1984; le Roux 1989). Differences between the species composition of the burn and the fire protection treatments were supported by the consistently large number of rare species unique to the fire protection treatment compared to the burn treatments at each site. Comparisons of the species composition between treatments also indicated that the burn treatments at each site were more similar to each other than to the fire protection treatment.

RESPONSES TO BURNING:

In the burn treatments, ordination showed that environmental gradients across each site were having a greater effect on the species composition of the plots than the treatments applied to them. Based on the similarity of the replicates of each treatment, when compared to replicates of all the other treatments, treatments appeared to be having the greatest effect at Cathedral Peak. This was supported by the distribution of species and rare species across the replicates of each treatment, being the most even at Cathedral Peak. However, there were no clear trends in degree to which treatments were determining the similarity in their species composition of their replicates, according to either the frequency or season of burn at any of the sites. Thus, no significant differences were found in either the alpha diversity or general species composition, after the long term application of a range of frequencies and seasons of burn, at any of the sites.

VEGETATION PATCHINESS AND THE EFFECT OF SCALE:

In the absence of species responding to either frequency or season of burn, and because post-burn differences had been accounted for, species turnover between treatments appeared to be the result of species/area relations. The lack of response to frequency and season of burn also accounted for the absence of clear trends in vegetation patchiness according to the burning regimes applied in the small plots at each site and the large plots at Honeydale. In the small plot studies, species rich treatments at small scales (high y-intercept values) were consistently found to include species at a slower rate as the sample area increased (slope values). Thus, at the smallest scale of measurement treatments differed, but as sample size increased, richness in the species poor treatments increased at faster rate than in the species rich treatments and so reduced the difference. This may explain why species richness appeared to respond to the burn treatments when considered as the mean of the replicates of each treatment but not when taken as the total richness across the replicates. Due to the directional succession of species in the fire protection treatments at each site, vegetation patchiness in these treatments could not be compared to that in the burn treatments.

BETA DIVERSITY:

A similar problem was encountered in sampling beta diversity in the Cathedral Peak catchments. Here the effects of different burning treatments on species compositional changes across the landscape were compared between catchments by standardising their beta diversity according to that in their adjacent fire-breaks. Whereas the burn treatments had coincided prior to sampling, so removing the effects of post-burn succession, directional succession was not accounted for in the fire protection treatments. However, vegetation patchiness in the octennial spring burn was higher than that in the biennial burns, although only marginally for the biennial summer and autumn burns. The effects of directional succession were also noted in the number of species unique to the catchment in transect pairs being highest in the fire protection treatments. The effects that annual burning in the fire-breaks had on species composition were found to differ most from those of the octennial burn. Where plants respond differently to fire, resulting in vegetation patchiness, the extent of this patchiness may be determined by which species are favoured by a particular burning regime (Bond & van Wilgen 1996). Thus, different species compositions favoured by biennial and octennial burning may explain the higher vegetation heterogeneity in the latter treatment. This measure of dissimilarity was, however, only of the presence/absence of species and thus not the strongest indicator of the effects of various burning treatments on species composition. In addition, with only two burn frequencies and the wide range of variation in vegetation heterogeneity across the biennial treatments the conclusion that vegetation patchiness increases with burn interval was not strongly supported.

FORBS AND BURNING:

Southern African grassland literature makes little reference to the either the taxonomic or morphological composition of the grassland forb flora. Therefore, to address this problem, at least for the sites examined, attempts were made to identify the species collected. The most striking finding of this exercise was that the majority of plants possessed some form of underground storage organs, a trait apparently common in fire prone systems (Burtt-Davy 1922; Martin 1966; West 1971; Rourke 1972; McMaster 1976; Carlquist 1977; Pate & Dixon 1981). Though fires may not have been the selective force driving the development of such structures, their presence conveys obvious selective advantages. Under frequent burning, it is predicted that storage organs would allow the plants to sprout and flower before they were shaded over by the grasses. In the absence of fire, a build up of moribund material in the sward may prevent the necessary warmth from reaching the ground to break the winter dormancy of some of the forbs (Bayer 1955). Thus, storage organs would have provided the forbs with the plasticity to deal with the variable fire regimes under which I speculate the grassland flora have evolved (Chapter

1.5). This ability to deal equally well across a range of burning regimes may therefore explain why species diversity and composition did not appear to respond to the burning treatments examined in my study.

GRASSES AND BURNING:

Measures of the aerial cover indicated that the sward canopy at each site was dominated by a few grass species. These species showed clear responses to fire frequency related to the site of tiller initiation. The cover constituted by the bunch grasses, whose tillers are borne above the soil surface (Everson *et al.* 1988), consistently increased with increasing burn frequency. Conversely, the cover constituted by the sod-forming species, whose tillers are borne at or below the soil surface (Everson *et al.* 1988), consistently decreased with increasing burn frequency. Interestingly, the rate at which the bunch grasses, particularly *Themeda triandra*, decreased with burn frequency was higher at Ukulinga than at the other two sites, where *T. triandra* was still well represented at burn intervals greater than two years.

Results from Ukulinga and Cathedral Peak showed that the bunch grass species performed better under autumn and winter than spring burning. Sod-forming species, at these two sites, generally seemed to do better in spring burn treatments. Though this trend appeared to be reversed at Honeydale, it has been supported by a number of studies in the southern African grasslands, particularly for the bunch grass, *T. triandra* (Staples 1926, 1930; Tainton & Mentis 1984; Everson *et al.* 1988; le Roux 1989). The results from Honeydale appear to be the first reported of the effects of burn season on sward cover for the arid grasslands.

SWARD STRUCTURE AND BIOMASS:

Though frequency and season of burn were found to influence the composition of the grass species that dominated the aerial cover of the sward, the effects of the long term application of short and long burn intervals had no significant impact on sward structure at any of the sites. Where differences were found, was according to the post-burn age. These were observed between the annual treatment and the replicates of the quinquennial treatment at Cathedral Peak, that had not been burnt for five years. Thus, sward biomass was found to accumulate with the time since last burn, a well noted phenomenon in the southern African grasslands (Tainton 1981; Tainton & Mentis 1984).

Trends in biomass could only be related to the influence of frequency and season of burn on the dominant grass species at Ukulinga. Here the proportional representation of one grass species, *Aristida junciformis*, appeared to be determining the response of biomass to the burn treatments applied across the site. An increase in biomass with decreasing burn frequency was shown at Ukulinga, in the winter treatment at Honeydale and the spring treatment at Cathedral Peak. The remaining treatments at Honeydale and Cathedral Peak, instead suggested that biomass decreased with burn frequency. Winter burns were, however, found to consistently produce higher biomass than the spring burns across all the sites, a result supported by studies in the KwaZulu-Natal Midlands (Tainton & Mentis 1984).

CONCLUSIONS AND RECOMMENDATIONS

There are a number of good reasons why the southern African grassland biome deserves a high conservation priority. The grasslands contain a diverse flora, including many rare and endemic species, with a major "hotspot" of diversity located in the montane regions of the Drakensberg (Cowling & Hilton-Taylor 1994). This biome also supports the largest urban population in the region, with its accompanying industrial and agricultural demands (O'Connor & Bredenkamp 1997). Further, less than two percent of the biome is currently being conserved, even though it shows a disproportionately high association between ecosystems, vegetation types and threatened plants compared to surrounding vegetation types (Scott-Shaw 1999).

As there is not much scope for increasing the area that is currently conserved in the immediate future, it is important that conservation areas be managed to maintain the maximum biodiversity. Central to the management of the grassland biome is the manipulation of the disturbance regime, and in particular, the burning regime. This is particularly relevant in the Drakensberg grasslands where herbivore densities are limited by hostile winter conditions, and fire is the only practical means of manipulating defoliation. As discussed in Chapter 1.5, large scale hominid influence in the southern African grasslands is very recent in evolutionary time. Compared to what is predicted to have been the natural burning regime, and that imposed by Stone Age peoples, the last 300 years have seen a radical shift in burning compared to what the flora evolved under. Based on this, questions have been raised as to the relevance of current burning regimes (designed to meet the needs of the grazier) to the objectives of the conservationist.

The results of this study indicated that diversity can be maintained under current burning practises. While the dominant grass species showed clear responses to frequency and season of burn, general species composition appeared to be more affected by environmental gradients than burn treatments. Measures of diversity were also found to be dependent on the scale at which they were performed and differences between sites. Thus, there was no support for the either the IDH or a response of vegetation patchiness to burning at the plot scale. At the landscape scale, beta diversity appeared to increase with longer burning intervals across the Cathedral Peak catchments, but this was only weakly supported by the narrow range of burn frequencies. However, species richness showed some evidence that it may display a humpbacked relationship to biomass across the grassland biome. The general lack of response to different burning regimes is not to say that forbs are not responding to fire, as many cases of post-fire flowering have been demonstrated in grassland taxa (Frost 1984). Therefore, where there are rare or endangered taxa with high conservation priority, appropriate fire regimes may be important, and these cases require detailed study.

In the absence of specific conservation objectives, burning regimes may be used to manipulate the dominant grass species, while still maintaining diversity. Nonetheless, it was noted that the dominant grasses declined faster at Ukulinga with changing burn intervals than at the other two sites. This implies that managers need to be more careful in the KwaZulu-Natal midlands as to the burning regime they choose than they would elsewhere in the biome. Results across the three study sites also suggested that biomass increases with increasing burn interval, although trends were not consistent according to the season of burn. Light attenuation results indicated that sward structure did not differ according to the long term application of short or long fire return intervals, but was influenced by the time since the last disturbance. These post-burn successional changes that the sward undergoes after a disturbance require further study. In particular, the succession of emerging and retreating forbs as they pass into and out of dormancy, or the seed bank, according to the season or the time since the last disturbance.

Although species composition did not differ according to the burning treatments, changes due to directional succession under fire protection resulted in a different suite of species being introduced. Thus, diversity on a landscape scale may be maximised by maintaining fire protected areas to promote species that would not be favoured by burning. The maintenance of fire protected areas would, however, be subject to management objectives. If the encroachment of woody species is undesirable, or fire protection promoted the introduction of alien plants (such as the *Lantana camara* in the Ukulinga fire protection plots - Figure 1.1), then burning would be recommended.

Unlike the agriculturally significant grasses that have been well studied, the burning responses of the grassland forbs have been largely ignored. It is hypothesised that the presence of underground storage organs, possessed by so many of the forbs, allows these plants to tolerate both short and long fire return intervals across a range of seasons. This may explain the general lack of response of species composition and diversity to the different burning regimes. Although noted as a common characteristic of species in fire prone systems (Burtt-Davy 1922; Martin 1966; West 1971; Rourke 1972; McMaster 1976; Carlquist 1977; Pate & Dixon 1981), these underground structures have received little attention in the southern African grasslands. Further, little record exists of the basic biology of the grassland forb flora. This poses serious implications for the conservation of our grasslands. Vigorous sprouting species in particular, are often poor recruiters (Bond 1998) and their biggest threat is habitat change, since if an individual dies, it is seldom replaced. Thus, although forbs may be buffered from disturbance by their underground storage organs, being poor recruiters, they would not be able tolerate habitat loss. This is particularly significant in a biome which arguably experiences the greatest industrial, urban and agricultural demands in southern Africa (Rutherford & Westfall 1994; O'Connor & Bredenkamp 1997). Therefore, to conserve the phytodiversity of the grassland biome, a better understanding of the modes of persistence and regeneration of the forb flora is required.

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